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Regional, ontogenetic, and sex-related variations in elastic properties of cortical bone in baboon mandibles

Qian Wang^{1,*}, Dennis W. Ashley², and Paul C. Dechow^{3,*}

¹ Division of Basic Medical Sciences, Mercer University School of Medicine, Macon, GA 31207

² Department of Surgery, Mercer University School of Medicine, Macon, GA 31207; Trauma Services, Medical Center of Central Georgia, Macon, GA 31201

³ Department of Biomedical Sciences, Baylor College of Dentistry, Texas A & M University System Health Sciences Center, Dallas, Texas 75246

Abstract

Understanding the mechanical features of cortical bone and their changes with growth and adaptation to function plays an important role in our ability to interpret the morphology and evolution of craniofacial skeletons. We assessed the elastic properties of cortical bone of juvenile and adult baboon mandibles using ultrasonic techniques. Results showed that, overall, cortical bone from baboon mandibles could be modeled as an orthotropic elastic solid. There were significant differences in the directions of maximum stiffness, thickness, density, and elastic stiffness among different functional areas, indicating regional adaptations. After maturity, the cortical bone becomes thicker, denser, and stiffer, but less anisotropic. There were differences in elastic properties of the corpus and ramus between male and female mandibles which are not observed in human mandibles. There were correlations between cortical thicknesses and densities, between bone elastic properties and microstructural configuration, and between the directions of maximum stiffness and bone anatomical axes in some areas. The relationships between bone extrinsic and intrinsic properties bring us insights into the integration of form and function in craniofacial skeletons and suggest that we need to consider both macroscopic form, microstructural variation, and the material properties of bone matrix when studying the functional properties and adaptive nature of the craniofacial skeleton in primates. The differences between baboon and human mandibles is at variance to the pattern of differences in crania, suggesting differences in bone adaption to varying skeletal geometries and loading regimes at both phylogenetic and ontogenetic levels.

Keywords

craniofacial skeleton; biomechanics; function; adaptation; Micro-CT; primate

Elastic properties and their variations in individuals are important for understanding bone adaptations and quality at the tissue level (Dechow et al., 1992, 1993; Dechow and Hylander, 2000; Schwartz-Dabney and Dechow, 2003; Wang and Dechow, 2006; Wang et al., 2006; Rapoff et al., 2008). They are especially indispensable for exploring the biomechanics and adaptation of primate skulls using Finite Element Analysis (FEA) (Strait et al., 2005, 2009; Wang and Dechow, 2006; Wang et al., 2006; Rayfield, 2007). We have

*Please send page proofs and direct correspondence to: Dr Qian Wang, Division of Basic Medical Sciences, Mercer University School of Medicine, 1550 College Street, Macon, GA 31207. Phone: 478-301,4043; Fax: 478-301,5489; wang_q2@mercer.edu. Dr Paul C. Dechow, Department of Biomedical Sciences, Baylor College of Dentistry, Texas A & M University Health Science Center, 3302 Gaston Ave, Dallas, TX 75246; Phone 214-370,7229; Fax 214-828,8951; pdechow@bcd.tamhsc.edu.

systematically collected elastic properties from the craniofacial skeletons of three species including modern humans (crania and mandibles), macaques (crania), and baboons (crania) (Peterson, 2002; Peterson and Dechow, 2003; Schwartz-Dabney and Dechow, 2002a, 2003; Wang and Dechow, 2006; Wang et al., 2006). Our findings suggest that (1) there are regionally specific cortical elastic properties among species, and (2) species-specific differences in regional variation of cortical elastic properties relate to differences in skull form. Thus, the knowledge of patterns of cortical elastic properties in primate craniofacial skeletons is likely to bring insights to functional morphology, taxonomy, and evolution in extant and extinct human and primate forms.

Study of ontogenetic changes in mechanical properties during skeletal growth furthers understanding of how bone geometric and elastic properties are adapted to morphology, function, ageing, pregnancy, and pathological conditions (Currey and Butler, 1975; Ekeland et al., 1982; Keller et al., 1985; Reid and Boyde, 1987; Stein, 1988; Currey et al., 1996; Hara et al., 1998; Currey, 2001; Ruff, 2003; Alippi et al., 2005; Havill et al., 2006; Elsalanty et al., 2008). Thus, two fundamental questions need satisfactory answers: [1] What is the pattern of the variation in bone material properties? [2] What is the mechanism behind the variation in bone material properties? Recently, the coupling of micro-CT imaging and ultrasonic assessment of 3D elastic properties in the cortical bone of a human mandible and femur (Dechow et al., 2008) demonstrated for the first time the important relationship between tissue elastic anisotropy and the spatial configuration of osteons. This finding reveals the structural basis of bone mechanical properties at the tissue level, in which the long axes of the osteons, as represented by the Haversian canals, are aligned with the axes of maximum elastic stiffness of the cortical bone (Dechow et al., 2008).

Mandibles are good models for studying bone elastic properties and their variation in anatomical regions with varying function. Studies in modern humans, the only species systematically examined to date, have demonstrated significant regional variations in cortical elastic properties (Schwartz-Dabney and Dechow, 2002a, 2003). Here we investigate the material properties of a second primate, *Papio hamadryas anubis*, in order to determine whether material properties of cortical bone assume a similar pattern of adaptation to function, and further how bone material properties change with growth in a primate mandible. Although published data are unavailable for cranial material properties, two studies that report bone strength of long bones in baboons (*Papio hamadryas cyanocephalus*) (Keller et al., 1985; Ruff, 2003) show that bone strength elasticity increases with age.

Baboons have an interesting craniofacial configuration with pronounced sexual dimorphism (Dechow, 1980; Leigh and Cheverud, 1991; Plavcan, 2001; Jolly, 2003). Baboon mandibles with their elongated corpora, large male canines, and well-excavated fossae of the mandibular corpora, have evolved in form since the Pliocene and are of special interest in studies of the biomechanics, adaptation, and evolution of primate mandibular structure (Hylander, 1985; Hylander and Johnson, 2005; Jablonski, 1993; Jablonski et al., 2002; Vinyard et al., 2006; Wall et al., 2006). We expect the study of cortical elastic properties in baboon mandibles of different ages and sexes should reveal important information about relationships between ontogeny, morphology, and function. We compared elastic properties between juvenile and adult specimens, and between adult male and female specimens, to glean information about changes in bone intrinsic biomechanical features during growth.

Moreover, we compared the cortical material properties from adult baboons to those from adult human mandibles (summarized from Schwartz-Dabney and Dechow, 2003) to reveal taxonomic differences, as in an earlier study on crania (Wang et al., 2006). Our past and ongoing studies of bone material properties in *Homo*, *Macaca*, *Papio*, *Pan*, and *Gorilla*

indicate that elastic properties of craniofacial bone can vary according to anatomical regions, and detailed comparisons of cranial cortical bone among modern human and two papionin species demonstrated that bone material properties are more similar in *Macaca* and *Papio* than they are between either of those species and *Homo*, indicating species-specific differences, and also patterns of similarity that reflect phylogeny (Wang et al., 2006; Strait et al., 2009). Humans and baboons differ in skull shape, due to adaptations to differences in masticatory and oral function through adjustments in cranial cortical bone mass, microstructure, and density. Mandibular variations have not been examined. In the postcranial skeleton, Ruff (2003) concludes that baboons have stronger limb bones relative to body size than humans at all stages of development. This assessment is based on cortical thickness and studies of geometric structural properties without consideration of material properties. It is likely, but untested, that cortical material properties are a lesser factor in functional postcranial differences. Our data suggest that adaptation of the material properties of craniofacial cortical bone may be more important in this regard. In the crania, baboons have thinner yet stiffer and less anisotropic cortical bone than humans (Wang et al., 2006).

We hypothesized that the ontogeny and the development of sexual dimorphism have a significant impact on cortical elastic properties in baboon mandibles that likely reflects differences in local tissue adaptation to altered shape and stress/strain patterns. In addition, bone intrinsic mechanical and extrinsic morphological features were compared to examine associations among some features of bone quality, form, and function, including relationships between orientations of the maximum stiffness and bone anatomical axes, and cortical density and cortical thickness. An inverse relationship between thickness and stiffness or density may suggest that bone strength is equivalent but that matrix distribution is altered, suggesting physiological responses to maintain structural stability (Wang et al., 2006). Likewise, an association between the orientation of maximum stiffness and aspects of microstructure, such as the orientation and size of osteons, may provide evidence concerning how bone material properties and microstructural variation are related. To test these hypotheses, we compare regional variations in elastic properties in the baboon mandibles by age and sex. Further, we compare the baboon patterns to those previously described in human mandibles.

MATERIALS AND METHODS

Cortical bone samples were removed from seven baboon crania of varying age and sex (Table 1). Three juvenile males, aged 2.9–4.7 years, were in group JM (Juvenile Male); two adult females, aged 18.0 and 20.1 years, were in group AF (Adult Female); two adult males with uncertain age but with a complete permanent dentition were in group AM (Adult Male). All were classified as *Papio hamadryas anubis*. All mandibles had intact alveolar ridges and lacked evidence of bone disease. All animal tissues were obtained from the Regional Primate Research Center (RPRC) at the University of Washington (supported by NIH grant RR00166). An extra specimen of an adult female baboon (also *P. h. a.*) for micro-CT analysis was obtained from the Southwest National Primate Research Center (supported by NIH-NCRR grant P51 RR013986). Animal tissue use conformed to all NIH, state, and federal standards. The tissues were stored in freezers at -20°C prior to removal of bone samples. Due to the lengthy period required for the collection of opportunistic specimens, cadavers were stored in a freezer for several years before specimens were processed. Although there are concerns over the effects of formalin fixation and freezing on the mechanical properties of bones (i.e., Evans, 1973; Sara and Williams, 1988; Zioupos et al., 2000; Nazarian et al., 2009), studies have reported that long term freezing does not have a measureable impact on cortical bone elastic properties measured ultrasonically (Evans, 1973; Zioupos et al., 2000). Further, if bone samples, including those fixed in formalin for no more than two weeks, are re-hydrated before testing, the bone elastic mechanical properties

have little alteration (Nazarian et al., 2009). In our study, cortical bone samples after preparation were kept hydrated in equal proportions of 95% ethanol and isotonic saline, which maintains the elastic properties of bone over time (Ashman et al., 1984; Zioupos et al., 2000). We were not able to obtain juvenile female specimens during this research. During the juvenile stage, male and female baboons have a similar cranial growth pattern prior to the development of the canine/sectorial premolar structures or before entering the growth spurt (Jolly, 2007), thus the juvenile male sample can be viewed as a reference for juveniles overall. Juvenile baboon females do have a slightly higher growth rate during the first two years of life (Johnson, 2003), but this minor difference in size by age is not relevant within the scope of this investigation. Fifty-two cortical samples were collected from the left half of each mandible: thirty samples from buccal side (B1 to B30) and twenty-two samples from lingual side (L1 to L22) (Fig. 1). On the buccal side, Sites 1–3 were collected from the symphysis; Sites 4–15 were collected from the corpus; Sites 16–30 were collected from the ramus. On the lingual side, Sites 1–3 were collected from the symphysis; Sites 4–15 were collected from the corpus; Sites 16–22 were collected from the ramus. On both sides, Sites 1–3 were located along the middle line at the symphysis; Sites 4–6 were under the C-P₁ or dc-dm₁ complex; Sites 7–9 were under dm₂/dm₃ in the juvenile or P₁/P₂ in the adult; Sites 10–12 were under M₁/M₂ in the juvenile or M₂/M₃ in the adult; Sites 13–15 were under the retromolar space immediately posterior to M₃ in the adult and to M₂ in the juvenile. Transverse mandibular breadth (TMB), or the thickness from the buccal side to the lingual side of the mandible, was measured at each of 52 sites of cortical bone samples using a digital caliper in AM1.

Positions of cortical specimens were selected to sample the whole surface of the cortex evenly and representatively. In the triangular fossa under the coronoid process, the bone structure is not bicortical with an endocortical space, but rather unicortical, so only one specimen could be collected, which is reported with other specimens taken from the buccal cortex of the cortical bone.

Sites were marked with a graphite line parallel to the lower border of the mandibular corpus (the mandibular plane). Bone cylinders with an inner diameter of 4 mm were harvested by means of a slow-speed dental handpiece and Nobelpharma trephine burs. In the craniofacial skeleton, cylindrical-shaped specimens are needed to insure accurate elastic property measurement because material orientation is unknown before testing (Schwartz-Dabney and Dechow, 2002b). Following specimen cutting, endosteal cancellous bone was removed with a Tormek water-cooled fine grinding wheel until there were no visible porosities on the endosteal surface. All cortical samples were measured with a digital caliper to the nearest 0.01 mm to verify diameter (4 mm) and determine cortical thickness, defined as the distance from the periosteum to the cortical-trabecular interface (Schwartz-Dabney and Dechow, 2003). Apparent density was calculated (mg/cm³) based on dry and wet weight measurements to the nearest 0.001 g with a Mettler-PM460 analytical balance and densitometry apparatus.

Thickness, density, and a set of longitudinal and transverse ultrasonic velocities were measured on each specimen to allow calculation of the elastic properties in three dimensions following Ashman et al. (1984), Schwartz-Dabney and Dechow (2003), and Wang and Dechow (2006). In this technique, longitudinal ultrasonic waves were generated by Panametrics V312-N-SU transducers resonating at 10 MHz. The transducers were powered with a Hewlett Packard Model 8100A pulse generator. Pulse delays induced by passage of ultrasonic waves through the bone were read on a Tektronix TD3012B digitizing oscilloscope. The bone cylinder was mounted on a 4-in Sherline Rotary Table (P/N 3700), which allowed accurate rotation to 0.1 degree. Pulse delays for each specimen were measured at 22.5-degree angular intervals up to 180 degrees. Ultrasonic velocities were

calculated by dividing the specimen thickness or diameter by the recorded time delay minus the standard system delay. To minimize error, all measurements were repeated twice, and the mean value of the two measurements was used for analysis, unless they showed large differences, and then measurements were repeated until consistent results were obtained. Samples which gave readings with inconsistencies greater than 5% were discarded.

A refined method of determining the axes of minimum and maximum stiffness in the plane of the cortical plate was used. A program written in Mathcad (version 2001) was used to fit the calculated longitudinal velocities and their angular orientation for each bone specimen to a sine function ($a \cdot \sin [X + b] + c$) (Wang and Dechow, 2006). The coefficients a , b , and c corresponded to the orientation of the maximum deviation of the curve from the average velocity, the axes of maximum stiffness, and the average velocity respectively. The direction of the axis of maximum stiffness (axis of E_3) corresponded to the direction of peak longitudinal velocity. Likewise, the minimal principal axis (axis of E_2), or least stiffness direction, corresponded to the lowest velocity. The third axis (axis of E_1) was always tangential or perpendicular to the cortical plane. Correlation coefficients were generated and tested for significance for each plot between measured values and the idealized sine curve as generated by the sinfit function. For specimens that showed larger deviations from the sine functions, we examined the curves to assess if they were symmetrical, whether they had broad peaks and troughs, and whether the peaks and troughs maintained a 90-degree separation from each other. Axes of E_1 , E_2 , and E_3 served as three orthotropic axes to form three planes. Six transverse velocity measurements (V_{12} and V_{21} , V_{13} and V_{31} , V_{23} and V_{32}) could then be measured using Panametrics V156-RM transducers (5.0MHz) in the correct orientations for calculating technical constants (Note: In our notation, “ V ” is velocity here while “ v ” is Poisson’s ratio).

Elastic coefficients and technical constants were calculated numerically from cortical density and the longitudinal and transverse velocities (Ashman et al., 1984; Dechow et al., 1993), using a program written in Mathcad.

Technical constants include the elastic moduli, shear moduli, and Poisson’s ratios. Elastic moduli (E_i) measure axial stiffness or the amount of deformation (strain) relative to an applied load (stress). Subscripts, as in E_1 , E_2 , or E_3 , indicate the appropriate axis for each elastic modulus. Similarly, the subscripts indicate orientation for shear moduli and Poisson’s ratios. Shear moduli (G_{ij}) measure stiffness in shear or angular deformation relative to applied shearing loads in a plane indicated by the subscripts (G_{12} , G_{31} , or G_{23}). Poisson’s ratios (v_{ij}) are a measure of stiffness of a structure perpendicular to that of the applied load. It is a ratio of the strain in the secondary direction (response direction) divided by strain in the primary direction (applied load direction). The first subscript indicates the axis of the applied load and the second subscript indicates the response direction (v_{12} , v_{13} , v_{23} , v_{21} , v_{31} , v_{32}).

Ultrasonic velocities and densities were used to calculate 6×6 matrices, or “ C ” matrices, including nine unique elastic coefficients (c_{11} , c_{22} , c_{33} , c_{44} , c_{55} , c_{66} , c_{12} , c_{13} and c_{23}) from which twelve technical constants, including three elastic moduli (E_1 , E_2 , E_3), three shear moduli (G_{12} , G_{31} , G_{23}), and six Poisson’s ratios (v_{12} , v_{21} , v_{13} , v_{31} , v_{23} , v_{32}) were calculated. A consequence of the assumption of orthotropic material symmetry is that $v_{ji}E_i = v_{ij}E_j$. Thus, only three Poisson’s ratios were reported in this paper. These are given here as v_{12} , v_{13} , and v_{23} . We also compared relative stiffness between axes by using ratios of elastic moduli (E_1/E_2 , E_1/E_3 , E_2/E_3) to quantify anisotropy in the cortical planes.

To examine variation in the microstructure, three cortical samples from the symphysis, corpus, and ramus were imaged at a high resolution (6 μ m isotropic voxel size) using a

Scanco micro-CT imaging system (μ CT40, Scanco Medical, Bassersdorf, Switzerland). Raw data from scans are automatically reconstructed into two-dimensional grayscale images using a convolution back projection algorithm. These grayscale tomograms are then compiled into three-dimensional binary images using a Gaussian filter and a global threshold based on a histogram analysis of X-ray attenuation within the structures. Quantitative image analysis was performed using these images. Tissue volume, osteonal (Haversian) canal volume, average canal thicknesses, and cortical porosity were measured (Hildebrand et al., 1999; Cooper et al., 2003). Average hydroxyapatite (HA) mineral density for the specimens was calculated based on the calibration of X-ray attenuation to HA standards.

Data were analyzed using the Minitab statistical analysis program 14.1 (Minitab, Inc., State College, PA). Descriptive statistics, including means and standard deviations, were calculated for all measurements. Comparisons included: (1) within mandible comparisons among 4 functional areas (symphysis, area under canine, corpus, and ramus) within sex-age groups; and (2) among sex-age group comparison. To determine if there were significant differences, a set of MANOVAs were performed ($\alpha = 0.05$) that took into account multiple factors, such as age, sex, and regions. Tukey's post hoc tests were used to check pair wise differences. Angular measurements (orientation of maximum stiffness) were analyzed with circular descriptive statistics, including the mean angles, circular SD, and Rayleigh's test of uniformity (Fisher, 1993), using the Oriana Statistical Analysis Program (version 2.02). The Rayleigh's test of uniformity revealed whether a site actually had a significant mean angle (oriented site) or whether the distribution of angles between individuals could not be distinguished from a random distribution (non-oriented site).

RESULTS

Variation of cortical thickness and elastic properties within mandibles

Throughout the mandible, there were significant differences in cortical thickness and density (Table 2, PFig. 2; Appendix Tables 1–7). The symphysis had the thickest cortical bone in all sex-age groups ($P = 0.005$). The ramus had the second thickest cortical bone in JM, while it had cortical bone as thick as the corpus in the adult male (AM) group, or had the least thick cortical bone in the adult female (AF) group.

The density, on the contrary, had a reverse pattern of variation. It was lowest in the symphysis, and increased posteriorly, except in the JM group, whose density in the area under dc-dm₁ and corpus was significantly higher than in the symphysis and ramus ($P \leq 0.017$). In AM, density in the corpus and ramus was significantly higher than that in the symphysis ($P < 0.001$), and in the area under C-P₁ ($P = 0.015$). In AF, density in the ramus was significantly higher than that in the rest of the mandible ($P \leq 0.022$); density in the corpus was significantly higher than in the symphysis ($P < 0.001$).

There was a negative correlation between cortical thickness and density, which was better demonstrated in individual mandibles (Fig. 3; Appendix Tables 1–7), except in AM2. AM1 showed the highest degree of correlation ($r = 0.773$, $P < 0.001$), primarily because of increased thickness and reduced density in the symphysis (Fig. 3). The correlation was greater in specific mandibles because some sites in the ramus in juveniles (JM1–2) and in the area under C-P complex and corpus in adult females (AF2) also had thick but less dense cortical bone (Fig. 3).

There were significant differences in elastic properties among four regions of the mandible in all three sex-age groups ($P < 0.03$) (Figs. 2,4); the degree of difference was large for material stiffness (elastic moduli and shear moduli), and relatively small for Poisson's ratios.

The patterns of regional differences in material stiffness were similar to that of cortical density. Without exception, in all sex-age groups, the cortical bone was least stiff in the symphysis and stiffest in the corpus. In the ramus, cortical stiffness was close to that of the symphysis in JM, but it was close to the corpus in adult animals. The ratio E_2/E_3 showed that the cortical bone in the corpus and ramus was more anisotropic than in the symphysis. Most sites with greater anisotropy were located along the lower border of the corpus and the posterior border of the ramus (Fig. 4).

There were significant differences in the orientation of the axis of the maximum stiffness among the four regions ($P < 0.01$) (Figs. 4–5; Appendix Tables 1–7). Relative to the occlusal plane, the grand mean axis of the maximum stiffness was 91.3° ($SD = 24.1^\circ$, $N = 37$, Rayleigh test of uniformity $P < 0.001$) in the symphysis, 96.2° ($SD = 42.7^\circ$, $N = 18$, $P = 0.01$) under C-P₁, -3.00° ($SD = 20.9^\circ$, $N = 143$, $P < 0.01$) in the corpus, and 51.8° ($SD = 35.7^\circ$, $N = 97$, $P = 0.01$) in the ramus in the JM and AF groups combined (Ramus I site in Fig. 5, sites adjacent to the sigmoid notch not included), and 59.1° ($SD = 35.2^\circ$, $N = 36$, $P = 0.01$) in the ramus of AM (Ramus II in Fig. 5). The difference in the grand mean orientation of maximum stiffness in Ramus I and Ramus II ($P = 0.08$) corresponded to the difference between the angles formed by the ramus and the mandibular plane in JM+AF and AM (Fig. 4). At the symphysis, the orientation of maximum stiffness ran consistently superior-inferiorly. In the corpus and ramus, the orientation of maximum stiffness approximated the long axis of the bone. The axis of the sites along the alveolar and basal borders of the corpus, or along the anterior and the posterior borders of the ramus, was generally parallel to the border outline. At the central parts of the corpus and the ramus, there was more variation in orientation.

There were similar significant correlations in most mandibles among extrinsic morphological shape measurements and intrinsic mechanical features. For example, in AM1, transverse mandibular breadth (TMB) correlated with cortical thickness ($r = 0.62$, $P < 0.001$) (Fig. 6a), density ($r = 0.64$, $P < 0.001$) (Fig. 6b), and E_3 ($r = 0.59$, $P < 0.001$) (Fig. 6d). Likewise, cortical thickness correlated with maximum stiffness (E_3) ($r = 0.62$, $P < 0.001$) (Fig. 6c). These correlations suggest that variations in loading patterns that depend on local shape differences are reflected in internal cortical structure and elastic properties.

Difference in cortical thickness and elastic properties among sex-age groups

Over the entire mandible, the adults had significantly higher values in cortical density, elastic moduli, and shear moduli than in the juveniles (MANOVA, $P < 0.001$) (Figs. 2, 7). Differences in Poisson's ratios and anisotropy ratios were much less although still significant. Interestingly, cortical thickness did not differ between JM and AF, but the difference was significant between AM and JM and between AM and AF (1.27 times greater; $P < 0.001$). In whole mandible, compared to JM, the density was 1.12 times higher in AF, and 1.14 times higher in AM, and E_3 was 1.31 (AF) and 1.35 (AM) times higher respectively.

If these variables are examined regionally, there are some interesting specific differences. In the symphysis, the differences in density, and elastic properties were not significant among the three groups (Fig. 7a). However there were shape difference; AM had stouter symphysis than AF and JM. For example, the index of the shape of symphysis ($100 \times \text{symphysis width} / \text{symphysis height}$) was 49–54 in AM, while it was around 40 in AF. Similarly, cortical bone was significantly thicker in AM ($3.29 \pm 0.32 \text{ mm}$) than in AF ($2.53 \pm 0.34 \text{ mm}$) ($P = 0.01$).

In the area under dc-dm₁ (juvenile) and C-P₁ (adult) (Fig. 7b), the overall differences in cortical thickness, density, and elastic properties between juvenile and adult animals were also significant ($P < 0.05$). Differences between AM and AF were not significant.

The overall differences between juvenile and adult animals was larger in the corpus ($P<0.0001$) (Fig. 7c). The overall difference between AM and AF was also significant ($P<0.004$). Cortical density and stiffness in AM were significantly higher than in AF in the corpus ($P<0.04$). Males had taller corpus (Table 1; Fig. 4) and a more well developed fossae, which in AM1 extended from under P_1 to under M_2 antero-posteriorly. In this area, the cortical bone was very thin and stiff. For example, Site F8 in AM1 was 1.42 mm in thickness and E_3 was 32.2 GPa.

In the ramus, the differences in density between the juveniles and the adults was larger than in any other region, and the differences in overall elastic properties was significant ($P<0.0001$) (Fig. 7d). The overall difference in elastic properties between the males and the females was less but also significant ($P<0.04$).

Variation of microstructural patterns

Overall, the microstructural patterns corresponded with anisotropic elastic properties. Osteonal/Haversian canals were oriented along the axis of the maximum stiffness, and the differences in porosity were likely due to both the number and size of the osteonal canals and resorption spaces (Table 3; Fig. 8). The ramus had high apparent density, mineral content, and very limited and small osteonal canals, while the symphysis had relatively low density and mineral content, and large osteonal canals and resorption spaces.

Comparison of cortical density, thickness, and elastic properties between human and baboon mandibles

Overall, there were significant differences in cortical thickness and elastic properties among human and baboon mandibles, yet there were similar significant regional differences (Table 4, PFig. 9). Both species have similar patterns of variation in cortical densities, except that baboons had greater overall variation (baboon: $CV=0.116$; human: $CV=0.055$) due to the lumping of adult males and females with apparent sex differences, which was not observed in the human mandibles. Cortical density of the symphysis is lowest in both humans and baboons. Baboons had significantly lower density in all areas anterior to ramus (≤ 0.041).

Adult human and baboon mandibles of the two sexes combined have similar patterns of variation in cortical thickness. Both have the thickest cortical bone at the symphysis, and the least thick cortical bone at the ramus. The differences in mean cortical thickness between human and baboon mandibles was insignificant except in the corporal area, where baboons have thicker cortices ($P=0.05$); the thickness at the ramus were comparable in the two species. The negative correlation between cortical density and thickness were not significant in the human mandibles, which might be due to the lesser regional differences, especially in thickness.

Elastic stiffness and anisotropy had different patterns among human and baboon mandibles by area (Table 4, Fig. 9). Both have similar E_1 s except at the symphysis, where baboons had lower values ($P=0.05$). For E_2 s, baboons had smaller values at all areas ($P\leq 0.05$). E_3 s were lower in the anterior region but were higher in the posterior region of the baboon mandibles ($P\leq 0.01$). Ratios of E_2/E_3 showed greater anisotropy in the cortical bone of baboon mandibles (grand mean and SE: 0.62 ± 0.01) compared to human mandibles (0.82 ± 0.01) ($P<0.001$), contrary to the crania, in which baboons were less anisotropic than humans.

DISCUSSION

Regional variation and functional implications

Our results demonstrated patterns of variation in elastic properties of cortical bone in baboon mandibles of three sex-age groups. The area-specific patterns of cortical thickness and elastic properties appear to correspond with functional differences.

The symphyseal cortex was thicker yet less stiff and less anisotropic than other regions. This area resists wishboning during mastication and is subject to a variable range of loading regimes depending on oral function and bite point (Hylander, 1979a,b,c, 1988; Daegling and McGraw, 2009; Daegling et al., 2009). Recent studies on symphyseal strength demonstrate that baboon mandibles need up to 1.4 kN to reach failure during the wishboning loading experiments (Vinyard et al., 2006). Thick cortex might allow resistance to deformation and increased strength when possible loads are more variable in orientation, thus the lesser stiffness of the symphysis may reflect a decreased material density but not necessarily decreased structural strength (Dechow and Hylander, 2000; Daegling and McGraw, 2009; Daegling et al., 2009). This raises an excellent question for further testing with finite element analysis that would need to incorporate the cortical material properties described here, and information on the structure and density of the more porous internal structure of the symphysis, which remains to be investigated.,

The corpus resists bending and twisting forces during function and direct compression and shear near the bite point in positions where the masticatory muscles are able to exert the greatest forces (Hylander, 1979a,b,c, 1988). Highest elastic and shear stiffness in this area resists deformation and may correspond with greater structure strength through increased mineralization (apparent density).

The opposite phenomenon in the symphysis and the ramus indicates that there may be a balance between bone thickness and bone stiffness/anisotropy. It is likely that there are a range of different strategies for increasing bone or structural strength, varying from [1] developing thicker yet less stiff and less anisotropic bones to [2] developing thinner yet denser and more anisotropic bones. We suggest that such variations may relate to variability in loading patterns locally within bones, such that greater variance in stress and strain orientations in three dimensions may lead to thicker but less stiff cortical structure and associated denser and more complex trabecular structure.

The cortical material behavior in the ramus differs between young and old animals, corresponding to the growth of the masticatory muscles. As in human crania (Peterson and Dechow, 2002), cortical bone in the muscle bearing region, the ramus, was more anisotropic than that in the non-muscle bearing regions in human and baboon mandibles (Figs. 2,9), which might suggest interactions between bone and adjacent muscular tissues. The area under dc-dm₁, or C-P₁, shows transitional features between those of the symphysis and the corpus, following the functional transition between these regions. The microstructural configuration patterns of orientations of cortical bone in different areas agreed well with the variation of elastic properties, as observed by Dechow et al. (2008), not only in porosity fraction, but also in the size of the porosities in our limited sample. The phenomenon of area-specific cortical elastic properties is found in other species in our investigations, such as in human skulls (Peterson and Dechow 2002; Schwartz-Dabney and Dechow, 2003) and in rhesus macaque and baboon crania (Wang and Dechow, 2006; Wang et al., 2006). These findings suggest that specific geometric differences in skeletal form relate to differences in area-specific cortical elastic properties in primate craniofacial skeletons, and therefore demonstrate the integration of bone intrinsic and extrinsic features.

Ontogenetic perspective on elastic properties

During growth in baboons, mandibles become longer (posteriorly), higher (inferiorly), and transversely wider in both males and females (Fig. 10) (Schneiderman, 1992; Enlow and Hans, 1996). In material properties, adult animals have denser, stiffer, but less anisotropic cortical bone than juvenile animals. The degree of this difference varies by area, being small in the anterior areas, intermediate at the corpus, and largest in the ramus. Therefore, baboon mandibles, like other skeletal parts of various species, increase in bone density and strength during growth (Currey and Butler, 1975; Keller et al., 1985; Currey et al., 1996; Hara et al., 1998; Currey, 2001; Ruff, 2003; Havill et al., 2006), owing to increased mineralization and collagen-crossing link of bone matrix.

However, it is interesting to observe that juvenile baboons have less dense but more anisotropic cortical bone than the adult baboons, in contrast to elastically isotropic bones in immature canine mandibles (Ashman et al., 1984). Generally males and females have similar patterns of change, especially in the corpus and ramus (Fig. 7). The amount of change varies from area to area; the most dramatic being in the ramus, followed by the corpus, then the symphysis; the least change is detected at the area under C-P₁. The widening of the angle between the axes of maximum stiffness in the ramus and the mandibular plane (Figs. 4, 9) corresponds to the widening of the angle between the corpus and ramus in the adult males, as an effective way to lengthen the mandible to increase the gape for the development of the canine-premolar complex in male baboons (Table 1; Figs. 4, 9). There is no distinct change in adult females in this regard corresponding with the lack of development and specialization of the canines.

Adaptation of elastic properties to sexual dimorphism

The C-P₁ complex in baboons is highly sexually dimorphic with the development of canines and first premolars in the adult males. However, there is no significant difference in overall elastic properties between adult males and females in the area under the C-P₁ complex. Male canine function might have little or no effect on the elastic properties of cortical bones covering the root of the canines, but males have relatively thinner cortical bone in this region. Whether this indicates this area experiences low functional stresses corresponding with the enlargement of the canine root or not awaits further study. The enlargement of the mandible obviously needs stronger muscle force for action, which might be responsible for denser and stiffer cortical bone in both corpus and ramus in adult males than in adult females. The corpus experiences twisting about the long axes during unilateral mastication and incision, yet the corporal fossa can develop at the central part of the corpus, which, being close to the neutral axis, does not need to resist high bending or twisting forces (Hylander, 1979a,b,c, 1988; Daegling and Hylander, 2000), and might be stress-shielded by loads carried by the canine root itself. Adult male baboons have taller corpora providing a larger central part of the mandible for developing a fossa. The elongation of mandibles in male animals also increases the moment arm lengths for incisor and molar biting. The mandibles of the male animals have associated adaptations in both material (stiffer) and structural (taller) features. The significance and underlying causes, especially the effects of allometry and sexual dimorphism, of variation in cortical thickness, density, and elastic properties in male mandibles awaits further investigation.

Integration of skeletal morphological and mechanical features

There were significant correlations among extrinsic morphological and intrinsic mechanical features of the mandible including: 1) anatomical axis and the orientation of maximum stiffness; 2) gross morphological dimensions and cortical thickness, density, and elastic stiffness; and 3) patterns of bone elastic properties during ontogeny and sexual dimorphism. These suggest integration of skeletal morphological, functional, and mechanical features.

The significant negative correlation between cortical density and thickness in baboon mandibles has been observed in human mandibles (Schwartz-Dabney and Dechow, 2003) and macaque crania (Wang and Dechow, 2006). This negative correlation is also observed at the species level, baboons having thinner yet denser cortical bones in craniofacial skeletons than macaques and humans (Wang et al., 2006). This inverse relationship between thickness and stiffness suggests that bone strength may be equivalent but that matrix distribution is altered, suggesting biomechanical consequences that may be related to patterns and variability in loading in different parts of the skeleton (Wang et al., 2006).

Comparison of human and baboon cortical material properties

In all regions, baboon mandibles have cortical bone that is more anisotropic than human mandibles, contrary to the opposite pattern in crania (Wang et al 2006). This difference in anisotropy varies between regions and orientations. Radial elastic moduli (E_1) are similar between humans and baboons, except at the symphysis, where baboon moduli tend to be less, corresponding with the lower elastic moduli in all directions, and decreased density in baboons. This difference at the symphysis may relate to functional and developmental differences in jaw loading patterns between baboons and humans that are beyond the scope of this discussion. But note in this regard that we know relatively little about in vivo loading patterns in the human symphysis; for instance whether humans experience lateral transverse bending loads during mastication and the extent to which the human symphysis behaves as a curved beam (Daegling et al., 2009).

In the corpus and ramus, the greater anisotropy in baboon mandibular cortical bone reflects relatively larger E_2 s in humans, compared to similar (ramus and under C-P₃ and) or larger E_3 s in baboons. E_2 is more similar to E_1 in the baboons than in humans, and thus the cortical bone approximates more closely a structure of transverse anisotropy, such as that found in the midshafts of remodeled long bones, rather than the orthotropy of human mandibular cortical bone, where values of E_2 tend to be about midway between E_1 and E_3 (Dechow et al., 2008). Comparisons of elastic properties in human mandibular and femoral cortical bone suggest that the orthotropy of human mandibular cortical bone at a supraosteal or bulk tissue level compared to transverse isotropy in femoral bone relates to greater variation in the orientation of intracortical canals (presumably Haversian canals) in the mandible in the plane of the cortical plate (Dechow et al., 2008). A comparison of intracortical canal orientations and their variations among human and baboon mandibles is necessary to explore this issue further. The results could be of great interest especially since evidence suggests that osteonal orientation is related to direction of loading (Petrtyl et al., 1996; Klein-Nulend et al., 2005; van Oers et al., 2008), and findings might ultimately be used to interpret loading patterns in cortical bone from fossils. Elastic orthotropy and the degree of intraspecimen variation in the orientation of intracortical canals might reflect the range and frequency of loading patterns regionally within skeletal organs. Differences among craniofacial bones and long bones might also be explored to examine the problem of how structural and material properties work together in functional skeletal adaptations.

There are differences in mechanical properties of long bones among primate species including humans, indicating phylogenetical influences on the correlation between functional morphology and locomotor or loading type (Ruff, 2003; Kikuchi and Hamada, 2009). Long bones in baboons have stronger limb bones structurally relative to body size than humans (Ruff, 2003) and they have stiffer cortical bone materially than humans in most of the craniofacial skeleton (Wang et al., 2006) and at some mandibular sites. Interestingly, density is more correlated with E_3 in human mandibles than in long bones (Rho, 1991, p.66). In another group of yellow baboons (*P. h. cyanocephalus*), the elastic modulus along the long axis of the femur (which is likely to be along the direction of E_3 as well) is highly correlated to the bone dry density and ash content (Keller et al., 1985). Similar comparisons

in baboons might be revealing yet no information of three dimensional elastic properties is available on the elastic properties of postcranial cortical bone tissues from any nonhuman primates.

In juvenile and adult baboon mandibles, cortical bone on the buccal side is overall thicker and denser than that on the lingual side. This finding differs from observations made on human mandibles (Schwartz-Dabney and Dechow 2003), where buccal cortical bone is often thicker but not denser. Such differences are likely to relate to structural and functional differences such as the different development of symphyseal structure, i.e. external buttressing by means of a chin in humans versus internal buttressing by means of a symphyseal shelf in baboons. Regional differences in cortical material properties among baboon and human mandibles might reflect cortical adaption during development or evolution to different loading regimes and associated skeletal geometries, but this is difficult to assess without better information about variation in regional patterns of loading and genetic effects on cortical structure to compare with information on material properties.

Significance of intra-individual and intra-sex-age group differences

Though the analyses used in this study were sufficient to demonstrate age, sex, and area differences in patterns of cortical material properties, caution is warranted because age structure and sample size are factors influencing the accuracy and precision of reflecting true age and sex variation and consequently statistical results (Foote, 1993; Konigsberg and Frankenberg, 2002; Konigsberg et al., 2002; Steadman et al., 2006). As the number of mandibular specimens was small (3 juvenile males, 2 adult males, and 2 adult females), the samples of functional regions of each sex-age group were lumped together for multiple comparisons. Thus two problems were incurred. First, this procedure overlooked the variations within individuals, which were normally large as demonstrated in the crania of rhesus macaques (Wang and Dechow, 2006). Second, this procedure overlooked the variations within sex-age groups, as different samples from a homologous region from the two or three mandibles were grouped, thus increasing the possibility of Type I error. For example, in individual mandibles, the coefficient of variation of three elastic moduli was around 30% in juveniles, and 20% in adults in this study, yet it decreased to around 10% in the three sex-age groups. Though intra-group differences require more specimens to increase statistical rigor, within group differences were insignificant in adults males (e.g., Apparent density: ANOVA, $P=0.539$), but significant in the juvenile group with three animals ($P=0.008$) and in adult female group with two specimens ($P=0.022$). Yet these intra-sex-age group differences were normally smaller than the inter-sex-age group differences, especially when viewed by anatomical region. However, in light of these intra-specimen and intra-sex-age group variations and the problems created by low sample size, the results of measurements from the individual cortical specimens of all seven mandibles are provided in Appendix Tables 1–7. Both individual and regional materials property data can be used to build FE models to study the functional effects of individual property variations and regional functional morphology in particular. The regional averaged data have demonstrated phylogenetic patterns (Wang et al., 2006), and have helped to increase precision and accuracy in various Finite Element Analyses (Strait et al., 2005; 2009). These data will greatly increase our confidence in analyzing bone mechanical behavior and further work on more primate species is necessary here.

Importance of understanding variation in cortical bone material properties

Many factors, including function, sex, age, species, and nutrition among others, influence the bone remodeling process, leading to variations in bone density and material properties (Cowin, 1986). Baboon mandibles show that variations of bone material properties are related to anatomical regions. The basis of this variation is microstructural and is

determined by the variations at different hierarchical levels in bone including osteonal organization and mineral density at a tissue level, and collagen and mineral organization and orientation at an ultrastructural level, and the interactions between them, as discussed in more detail elsewhere (Dechow et al., 2008).

Understanding relationships between bone extrinsic and intrinsic properties, requires consideration of gross morphology, material structure, and functional patterns, and it may help to explore the possibility of estimating bone intrinsic properties from gross structure and function, or vice versa. The mapping of three-dimensional elastic properties and microstructure of cortical bone is not only important for creating accurate functional models (FEM) of skeletal organs, to interpret skeletal strain patterns, but also for the potential to draw insights into the functional mechanisms of bone development, adaptation, and remodeling.

CONCLUSIONS

1. There are significant regional differences in cortical thickness, density, elastic properties, the axis of the maximum stiffness, and microstructural configuration patterns throughout the mandibles of baboons, suggesting that specific structural differences in skeletal form relate to differences in area-specific cortical elastic properties in craniofacial skeletons.
2. There is a negative correlation between cortical thickness and density in baboon mandibles, suggesting a mechanism of balancing bone mass and elastic properties in the adaptation to bone function.
3. There is a significant difference in elastic properties between young and adult animals. Changes in elastic properties with maturity differ by area with the greatest differences found in the ramus.
4. Adult males have thicker and stiffer cortical bone than adult females, demonstrating the effects of allometry and sexual dimorphism.
5. Baboon mandibles have patterns of anisotropy and stiffness that are different overall and by region than those in human mandibles.
6. Relationships among morphology, function, and patterns of elastic properties in craniofacial bones suggest an integration of skeletal extrinsic and intrinsic mechanical features. Specific hypotheses relating to such integration, and structural/functional similarities and differences require detailed experimental testing in local skeletal regions. Finite element analysis is an optimal way to incorporate the complexities of structural and material properties for such analysis.

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LITERATURE CITED

- Alippi RM, Olivera MI, Bozzini C, Huygens PA, Bozzini CE. Changes in material and architectural properties of rat femoral diaphysis during ontogeny in hypophysectomized rats. *Comp Clin Pathol*. 2005; 14:76–80.
- Ashman RB, Cowan SC, van Buskirk WC, Rice JC. A continuous wave technique for measurement of the elastic properties of cortical bone. *J Biomech*. 1984; 17:349–361. [PubMed: 6736070]
- Cooper DML, Turinsky AL, Sensen CW, Hallgrímsson B. Quantitative 3D analysis of the canal network in cortical bone by Micro-Computed Tomography. *Ana Rec Part B New Anat*. 2003; 274B: 169–179.
- Cowin, SC. Bone mechanics. Boca Raton: CRC Press; 1986.
- Currey, JD. Ontogenetic changes in compact bone material properties. In: Cowin, SC., editor. *Bone mechanics handbook*. 2. Vol. Chapter 19. Boca Raton: CRC Press; 2001. p. 1-16.
- Currey JD, Brear K, Zioupos. The effects of aging and changes in mineral content in degrading the toughness of human femora. *J biomech*. 1996; 29:257–260. [PubMed: 8849821]
- Currey JD, Butler G. The mechanical properties of bone tissue in children. *J Bone and Joint Surg*. 1975; 57A:810–814. [PubMed: 1158919]
- Daegling DJ, Hotzman JL, McGraw WS, Rapoff AJ. Material property variation of mandibular symphyseal bone in colobine monkeys. *J Morphol*. 2009; 270:194–204. [PubMed: 18946868]
- Daegling DJ, Hylander WL. Experimental observation, theoretical models, and biomechanical inference in the study of mandibular form. *Am J Phys Anthropol*. 2000; 112:541–551. [PubMed: 10918128]
- Daegling DJ, McGraw WS. Masticatory stress and the mechanics of “wishboning” in colobine jaws. *Am J Phys Anthropol*. 2009; 138:306–317. [PubMed: 18785632]
- Dechow. Ph D Dissertation. University of Chicago; 1980. Functional morphology of the craniofacial skeleton of baboons.
- Dechow PC, Hylander WL. Elastic properties and masticatory bone stress in the macaque mandible. *Am J Phys Anthropol*. 2000; 112:553–574. [PubMed: 10918129]
- Dechow PC, Nail GA, Schwartz-Dabney CL, Ashman RB. Elastic properties of human supraorbital and mandibular bone. *Am J Phys Anthropol*. 1993; 90:291–306. [PubMed: 8460653]
- Dechow, PC.; Schwartz-Dabney, CL.; Ashman, RB. Elastic properties of the human mandibular corpus. In: Carlson, DS.; Goldstein, SA., editors. *Bone biodynamics in orthodontic and orthopedic treatment*. Ann Arbor, MI: Center for Human Growth and Development; 1992. p. 299-314.
- Dechow, PC.; Chung, DH.; Bolouri, M. Relationship between three dimensional microstructure and elastic properties of cortical bone in the human mandible and femur. In: Vinyard, CJ.; Ravosa, MJ.; Wall, CE., editors. *Primate Craniofacial Function and Biology, Developments in Primatology Series*. Springer; New York: 2008. p. 265-292.
- Ekeland A, Engesoeter LB, Langeland N. Influence of age on mechanical properties of healing fractures and intact bones in rats. *Acta Orthop Scand*. 1982; 53:527–534. [PubMed: 7102268]
- Elsalanty ME, Por YC, Genecov DG, Salyer KE, Wang Q, Barcelo CR, Troxler K, Gendler E, Opperman LA. Recombinant human BMP2 enhances the effects of material used for reconstruction of large cranial defects. *J Oral Maxill Surg*. 2008; 66:277–285.
- Enlow, DH.; Hans, MG. *Essentials of facial growth*. Philadelphia: W. B. Saunders Company; 1996.
- Evans, F. Preservation effects. In: Evans, F., editor. *Mechanical properties of bone*. Springfield: Charles C. Thomas; 1973. p. 56-60.
- Foote M. Human cranial variability: A methodological comment. *Am J Phys Anthropol*. 1993; 90:377–379. [PubMed: 8460661]
- Guldberg RE. Considering of mechanical factors. *Ann NY Acad Sci*. 2002; 961:312–314. [PubMed: 12081927]
- Hara T, Takizawa M, Sato T, Ide Y. Mechanical properties of buccal compact bone of the mandibular ramus in human adults and children: relationship of the elastic modulus to the direction of the osteon and the porosity ratio. *Bull Tokyo Dent Coll*. 1998; 39:47–55. [PubMed: 9663031]

- Havill LM, Allen MR, Bredbenner TL, Burr DB, Nicoletta DP, Levine S, Warren DM, Mahaney MC. Age-related changes in trabecular bone mechanical and material properties in baboon vertebrae [Abstract]. *Am J Phys Anthropol Suppl.* 2006; 42:101–102.
- Hildebrand T, Laib A, Muller R, Dequeker J, Rueggsegger P. Direct three-dimensional morphometric analysis of human cancellous bone: Microstructural data from spine, femur, iliac crest, and calcaneus. *J Bone Min Res.* 1999; 14:1167–1174.
- Howells, WW. Cranial variation in man: A study by multivariate analysis of patterns of difference among recent human populations. Cambridge: Harvard University Press; 1973.
- Hylander WL. An experimental analysis of the temporomandibular joint reaction force in macaques. *Am J Phys Anthropol.* 1979a; 51:433–456. [PubMed: 532828]
- Hylander WL. Mandibular function in *Galago crassicaudatus* and *Macaca fascicularis*: an *in vivo* approach to stress analysis of the mandible. *J Morphol.* 1979b; 159:253–296. [PubMed: 105147]
- Hylander WL. The functional significance of primate mandibular form. *J Morphol.* 1979c; 160:223–240. [PubMed: 458862]
- Hylander WL. Mandibular function and biomechanical stress and scaling. *AM Zool.* 1985; 25:315–330.
- Hylander, WL. Implications of *in vivo* experiments for interpreting the functional significance of robust australopithecines' jaws. In: Grine, FE., editor. *Evolutionary history of the robust australopithecines*. New York: Aldine de Gruyter; 1988. p. 55-83.
- Hylander WL, Johnson KR. *In vivo* bone strain patterns in the zygomatic arch of macaques and the significance of these patterns for functional interpretations of craniofacial form. *Am J Phys Anthropol.* 1997; 102:203–232. [PubMed: 9066901]
- Hylander WL, Johnson KR. A preliminary analysis of occlusal events during mastication in baboons employing an intra-molar force transducer [Abstracts]. *Am J Phys Anthropol Suppl.* 2005; 40:120.
- Jablonski, NG. *Theropithecus*: The rise and fall of a primate genus. Cambridge: Cambridge University Press; 1993.
- Jablonski NG, Leakey MG, Kiarie C, Anton M. A new skeleton of *Theropithecus brumpti* (Primates: Cercopithecidae) from Lomekwi, West Turkana, Kenya. *J Hum Evol.* 2002; 43:887–923. [PubMed: 12473488]
- Jolly CJ. Cranial anatomy and baboon diversity. *Anat Rec.* 2003; 275A:1043–1047.
- Jolly, CJ. Baboons, mandrills, and mangabeys. In: Campbell, CJ.; Fuentes, A.; MacKinnon, KC.; Panger, M.; Bearder, SK., editors. *Primates in perspective*. New York: Oxford University Press; 2007. p. 240-251.
- Johnson SE. Life history and the competitive environment: trajectories of growth, maturation, and reproductive output among chacma baboons. *Am J Phys Anthropol.* 2003; 120:83–98. [PubMed: 12489139]
- Keller TS, Lovin JD, Spengler DM, Carter DR. Fatigue of immature baboon cortical bone. *J Biomech.* 1985; 18:297–304. [PubMed: 4019527]
- Kikuchi Y, Hamada Y. Geometric characters of the radius and tibia in *Macaca mulatta* and *Macaca fascicularis*. *Primates.* 2009; 50:169–183. [PubMed: 19110657]
- Klein-Nulend J, Bacabac RG, Mulle MG. Mechanobiology of bone tissue. *Pathologie Biologie.* 2005; 53:576–580. [PubMed: 16364809]
- Konigsberg LW, Frankenberg SR. Deconstructing death in paleodemography. *Am J Phys Anthropol.* 2002; 117:297–309. [PubMed: 11920365]
- Konigsberg LW, Herrmann NP, Wescott DJ. Commentary on McBride et al. Bootstrap methods for sex determination from the os coxae using the ID3 algorithm. *J Forensic Sci.* 2002; 47:424–426. [PubMed: 11908629]
- Leigh SR, Cheverud JM. Sexual dimorphism in the baboon facial skeleton. *Am J Phys Anthropol.* 1991; 84:193–208. [PubMed: 2021194]
- Nazarian A, Hermansson B, Muller J, Zurakowski D, Snyder B. Effects of tissue preservation on murine bone mechanical properties. *J Biomech.* 2009; 42:82–86. [PubMed: 19081098]
- Peterson J, Wang Q, Dechow PC. Material properties of the dentate maxilla. *Anat Rec.* 2006; 288A: 962–972.

- Petrtyl M, Hert J, Fiala P. Spatial organization of the haversian bone in man. *J Biomech.* 1996; 29:161–169. [PubMed: 8849809]
- Plavcan JM. Sexual dimorphism in primate evolution. *Yrbk Phys Anthropol.* 2001; 44:25–53.
- Rho, JY. Ph D Thesis. University of Texas Southwestern Medical Center; Dallas: 1991. Mechanical properties of human cortical and cancellous bone.
- Rapoff AJ, Rinaldi RG, Hotzman JL, Daegling DJ. Elastic modulus variation in mandibular bone: A microindentation study of *Macaca fascicularis*. *Am J Phys Anthropol.* 2008; 135:100–109. [PubMed: 18058791]
- Rayfield EJ. Finite Element Analysis and Understanding the Biomechanics and Evolution of Living and Fossil Organisms. *Annu Rev Earth Planet Sci.* 2007; 35:541–576.
- Reid SA, Boyde A. Changes in the mineral density distribution in human bone with age: image analysis using backscattered electrons in the SEM. *J Bone Miner Res.* 1987; 2:13–22. [PubMed: 3455153]
- Ruff CB. Ontogenetic adaptation to bipedalism: Age changes in femoral to humeral length and strength proportions in humans, with a comparison to baboons. *J Hum Evol.* 2003; 45:317–349. [PubMed: 14585245]
- Saha S, Williams PA. Effect of various storage methods on the dielectric properties of compact bone. *Med Biol Eng Comput.* 1988; 26:199–202. [PubMed: 3226176]
- Schneiderman, ED. Facial growth in the rhesus macaque: a longitudinal cephalometric study. Princeton: Princeton University Press; 1992.
- Schwartz-Dabney CL, Dechow PC. Edentulation alters elastic properties of cortical bone in the human mandible. *J Dent Res.* 2002a; 81:613–617. [PubMed: 12202642]
- Schwartz-Dabney CL, Dechow PC. Accuracy of elastic property measurement in mandibular cortical bone is improved by using cylindrical specimens. *J Biomech Eng.* 2002b; 124:714–723. [PubMed: 12596640]
- Schwartz-Dabney CL, Dechow PC. Variations in cortical elastic properties throughout the human dentate mandible. *Am J Phys Anthropol.* 2003; 120:252–277. [PubMed: 12567378]
- Steadman DW, Adams BJ, Konigsberg LW. Statistical basis for positive identification in forensic anthropology. *Am J Phys Anthropol.* 2006; 131:15–26. [PubMed: 16485302]
- Stein MS. Bone size and mechanics at the femoral diaphysis across age and sex. *J Biomech.* 1988; 31:1101–1110. [PubMed: 9882042]
- Strait DS, Wang Q, Dechow PC, Ross CF, Richmond BG, Spencer MA, Patel BA. Modeling elastic properties in finite element analysis: How much precision is needed to produce an accurate model? *Anat Rec.* 2005; 283A:275–287.
- Strait DS, Weber GW, Neubauer S, Chalk J, Richmond BG, Lucas PW, Spencer MA, Schrein C, Dechow PC, Ross CF, Grosse IR, Wright BW, Constantino P, Wood BA, Lawn B, Hylander WL, Wang Q, Byron CD, Slice DE, Smith AL. The feeding biomechanics and dietary ecology of *Australopithecus africanus*. *Proc Natl Acad Sci USA.* 2009; 106:2124–2129. [PubMed: 19188607]
- van Oers RFM, Ruimerman R, Tanck E, Hilbers PAJ, Huiskes R. A unified theory for osteonal and hemi-osteonal remodeling. *Bone.* 2008; 42:250–259. [PubMed: 18063436]
- Vinyard CJ, Ravosa MJ, Hylander WL. Oh monkey, what a strong jaw you have: A preliminary comparison of symphyseal strength across monkeys, galagos and non-primate mammals [abstract]. *Am J Phys Anthropol Suppl.* 2006; 42:182–183.
- Wall CE, Vinyard CJ, Johnson KR, Williams SH, Hylander WL. Phase II jaw movements and masseter muscle activity during chewing in *Papio anubis*. *Am J Phys Anthropol.* 2006; 129:215–224. [PubMed: 16278877]
- Wang Q, Dechow PC. Elastic properties of external cortical bone in the craniofacial skeleton of the rhesus macaque. *Am J Phys Anthropol.* 2006; 131:402–415. [PubMed: 16617434]
- Wang Q, Strait DS, Dechow PC. A comparison of cortical elastic properties in the craniofacial skeletons of three primate species and its relevance to human evolution. *J Hum Evol.* 2006; 51:375–382. [PubMed: 16905178]
- Zar, JH. Biostatistical analysis. 4. Upper Saddle River, NJ: Prentice Hall; 1999.

Zioupou, P.; Smith, CW.; An, YH. Factors affecting mechanical properties of bone. In: An, RA.; Draughn, RA., editors. Mechanical testing of bone and the bone-implant interface. New York: CRC Press; 2000. p. 65-85.

Fig. 1.
Location of sites the baboon mandibles in lingual (Upper) and buccal (Lower) views.

Fig. 2. Baboon mandibular cortical thickness and elastic properties by anatomical region and sex-age group. Abbreviations: sym- Symphysis; C-P1- Area under dc-dm₁ or C-P₁ complex; corp- Corpus; ram- Ramus. Error bar: SE. Error bars are one sided to increase graph readability.

Fig. 3.

Negative correlation between cortical thickness (Th) and density (P). a - JM1: $P = -117.37 * Th + 1832.0$, $r=0.643$, $P<0.001$; b- JM2 : $P = -154.79 * Th + 1953.60$, $r=0.571$, $P<0.001$; c- JM3 : $P = -114.30 * Th + 1912.27$, $r=0.440$, $P=0.001$; d- AM1: $P = -156.006 * Th + 2281.99$, $r=0.773$, $P<0.001$; e-AF1 : $P = -88.54 * Th + 2015.60$, $r=0.423$, $P=0.002$; f- AF2 : $P = -136.99 * Th + 2177.66$, $r=0.653$, $P<0.001$. Abbreviations: sym- Symphysis; corp + C-P: Corpus plus the area under dc-dm₁ or C-P₁ complex; ram- Ramus.

Fig. 4. Magnitudes and axes of E_2 and E_3 in cortical bone samples on the lingual and buccal surfaces of each of the seven baboon mandibles.

Fig. 5. Mean orientation of maximum stiffness (E_3) in four areas. Area under C-P₁ contains only the buccal sites. JM and AF are grouped together as Ramus I, AM is Ramus II. Mean orientation of the axis of maximum stiffness on the corpus and ramus corresponds with the anatomical axis of the bone. However, variation exists at individual sites.

Fig. 6.

The correlation among skeletal extrinsic morphological and intrinsic elastic properties in AM1. Abbreviations: Th- Thickness, P- Density, MTB- Mandibular transverse breadth. a. $Th = 1.30 + 0.135 * MTB$, $r=0.625$, $P<0.001$; b. $P = 2065.977 - 22.406 * MTB$, $r=0.64$, $P<0.001$; c. $E_3 = -3.9677 * Th + 34.053$, $r=0.62$, $P<0.001$; d. $E_3 = 29.234 - 0.628 * MTB$, $r=0.59$, $P<0.001$.

Fig. 7.

Standardized magnitudes of differences in cortical thickness, density, and elastic properties between juvenile and adult animals. Values of JM are the standard with their SEs serving as transformation factors. For example, the normalized density value in the group AM = $(\text{Mean Density}_{\text{AM}} - \text{Mean Density}_{\text{JM}}) / \text{S.E. of Mean Density}_{\text{JM}}$. Thus the unit for the Y axis is the standard error of the mean of JM values. The X axis ($y = 0$) is for JM. This figure demonstrates not only how bone elastic properties differ between juvenile and adult animals, but also between adult male and female animals.

Fig. 8.

Microstructural images (resolution: 6 μ m isotropic voxel size) of three cortical samples from the buccal side of a female baboon mandible. a: symphysis; b: corpus; c: ramus. In all three anatomical regions illustrated, all specimens are oriented along the axis of maximum stiffness, which is similar to the long axis of the bone. Qualitatively, the orientations of osteonal canals are also seen to correspond with the axis of maximum stiffness. There were remarkable difference in porosity in the three regions, with the symphyseal region being especially more porous. In the symphysis, porosities include a greater region of nonmineralized voids in the bone in addition to the osteonal canals.

Fig. 9. Comparison of cortical thickness (a), density (b), elastic moduli (c–e), and anisotropy (f) between human and baboon mandibles. Error bar: SE. Abbreviations: see Fig. 2.

Fig. 10.

The superimposition of mandibles of JM1, AF1 and AM1 demonstrates the effects of growth and sexual dimorphism in baboon mandibles. The mandibles of the adult male and female baboons differ not only in length, but also in the slope of the ramus related to the mandibular plane. The mandibles were aligned horizontally on the mandibular plane and anteriorly along a line through the anthropometric landmark infradentale (id) oriented perpendicular to the mandibular plane.

Table 1

Cranio-metrical measurements of mandibles of baboons

	JM1	JM2	JM3	AF1	AF2	AM1	AM2
Age (years)	2.60	3.09	4.70	17.98	20.07	18-20 [/]	>20 [/]
Body mass (kg)	6.6	9.9	17.3	26.0	19.6		
Dental formula	I ₁ I ₂ cm ₁ m ₂ M ₁ (M ₂)	I ₁ I ₂ cm ₁ m ₂ M ₁ (M ₂)	I ₁ I ₂ cm ₁ m ₂ M ₁ M ₂	I ₁ I ₂ CP ₁ P ₂ M ₁ M ₂ M ₃	I ₁ I ₂ CP ₁ P ₂ M ₁ M ₂ M ₃	I ₁ I ₂ CP ₁ P ₂ M ₁ M ₂ M ₃	I ₁ I ₂ CP ₁ P ₂ M ₁ M ₂ M ₃
Bicondylar breadth	65.9	98.0	67.3	88.2	88.1	89.6	92.2
Corpus depth at M ₁	26.3	25.2	27.3	31.6	31.4	36.9	36.5
Corpus width at M ₁	11.9	10.2	11.6	8.9	11.2	11.0	14.5
Symphysis depth	29.5	32.0	37.4	39.5	44.6	39.9	54.2
Symphysis width	15.1	18.5	16.4	15.9	17.6	21.4	26.6
Ramus height	51.7	47.1	51.3	56.3	55.5	62.0	78.3
gn-go	52.8	69.5	60.4	73.1	80.4	96.5	83.2
Angle of mandible	121.1°	117.6°	114.9°	123.6°	123.0°	139.4°	130.4°

[/] Information on age and body mass of AM1 and AM2 was not available. Their age were estimated by dental status.

Abbreviations: cr-coronion, cd- condylion, id- infradentale, gn – gnathion, go- gonion.

Table 2

Area cortical thickness and elastic properties in baboon mandibles of three sex-age groups

Axis of E ₃ ⁵																
	N	P ¹	Th ²	E ₁ ³	E ₂ ³	E ₃ ³	G ₁₂ ³	G ₃₁ ³	G ₂₃ ³	v ₁₂ ⁴	v ₁₃ ⁴	v ₂₃ ⁴	E ₂ /E ₃	Buccal	Lingual	
JM	sym	Mean	1554.3	2.4	6.8	8.7	13.6	2.6	3.3	4.2	0.40	0.24	0.19	0.64	N.S.	94.0° (N=7)
		S.D.	137.6	0.7	1.3	2.2	2.4	0.7	0.6	0.9	0.11	0.05	0.06	0.12		16.6° (P<0.001)
	de-dm ₁	Mean	1723.8	1.3	9.9	11.1	16.9	3.8	4.3	5.2	0.35	0.30	0.20	0.67	77.1 (N=8)	N.A.
		S.D.	151.8	0.3	1.5	1.6	3.0	0.6	0.6	0.7	0.08	0.03	0.08	0.14	16.6 (P=0.003)	
	corp	Mean	1778.6	1.6	9.6	11.4	21.4	3.7	4.7	5.8	0.40	0.24	0.16	0.54	170.7° (N=27)	2.32° (N=34)
		S.D.	136.5	0.4	1.7	1.6	3.9	0.6	0.8	0.8	0.06	0.07	0.05	0.10	15.0° (P<0.001)	12.3 (P<0.001)
	ram	Mean	1567.1	2.0	7.4	8.8	16.1	2.9	3.6	4.5	0.38	0.24	0.16	0.55	52.7° (N=45)	129.1° (N=21)
		S.D.	138.3	0.9	1.5	2.0	2.6	0.7	0.6	0.9	0.11	0.06	0.07	0.10	18.0° (P<0.001)	25.7° (P<0.001)
AF	sym	Mean	1662.8	2.5	9.1	12.0	17.8	3.7	4.3	5.7	0.36	0.26	0.18	0.69	76.0° (N=6)	N.S.
		S.D.	134.1	1.2	1.5	2.2	3.8	0.7	0.7	0.8	0.07	0.03	0.07	0.14	18.4° (P=0.012)	
	C-P ₁	Mean	1787.0	2.2	11.9	14.2	19.6	4.6	5.5	6.6	0.38	0.27	0.20	0.73	N.S.	N.A.
		S.D.	128.3	0.8	1.7	1.7	1.9	0.5	0.7	0.8	0.05	0.02	0.05	0.10		
	corp	Mean	1890.6	1.9	12.4	15.2	25.2	4.8	5.9	7.6	0.39	0.26	0.17	0.61	0.5° (N=18)	177.6° (N=23)
		S.D.	126.4	0.6	1.7	2.0	3.7	0.6	0.8	0.9	0.06	0.06	0.06	0.13	26.3° (P<0.001)	14.4° (P<0.001)
	ram	Mean	1910.3	1.5	12.1	14.3	24.6	4.6	5.8	7.3	0.40	0.25	0.15	0.57	54.7° (N=28)	132.3° (N=13)
		S.D.	115.4	0.5	2.5	1.9	3.6	0.8	1.1	0.9	0.07	0.07	0.07	0.07	29.6° (P<0.001)	27.7° (P=0.004)
AM	sym	Mean	1620.8	3.3	9.3	11.0	16.9	3.5	4.5	5.3	0.39	0.23	0.20	0.65	92.1° (N=6)	95.0° (N=6)
		S.D.	109.8	1.1	1.9	1.9	2.8	0.7	0.9	0.9	0.07	0.07	0.07	0.07	7.7° (P<0.001)	11.1° (P=0.001)
	C-P ₁	Mean	1751.0	2.0	12.2	13.8	18.8	4.7	5.4	6.1	0.35	0.29	0.22	0.74	N.S.	N.A.
		S.D.	134.4	0.9	1.5	2.9	2.9	0.8	0.7	1.0	0.05	0.02	0.05	0.15		
	corp	Mean	1947.9	2.2	14.0	16.6	26.4	5.5	6.5	8.0	0.35	0.26	0.18	0.64	167.9° (N=18)	177.0° (N=23)
		S.D.	123.8	0.6	2.9	1.8	3.8	0.8	1.0	0.8	0.06	0.06	0.06	0.13	26.3° (P<0.001)	11.7° (P<0.001)
	ram	Mean	1955.4	2.2	12.5	14.5	25.3	4.7	6.0	7.2	0.38	0.23	0.18	0.58	56.7° (N=26)	121.7° (N=14)
		S.D.	87.3	0.6	3.2	2.3	3.0	0.9	1.0	0.9	0.07	0.07	0.07	0.07	25.9° (P<0.001)	24.0° (P<0.001)

¹P - density (mg/cm³);²Th - thickness (mm);

³ Unit for elastic (E) and shear modulus (G): Gpa (1 Gpa= 10^9 N/M²),

⁴ Poisson's ratios (ν) and anisotropic (E_2/E_3) values are unitless.

⁵ Axes of E_3 were related to the mandibular plane; Uniformity P -values for the mean axis of E_3 were derived from the Rayleigh test.

Abbreviations: JM – juvenile male; AF- Adult female; AM – Adult male; sym – symphysis; dc-dm1 in JM and C-P1 in AF and AM – area under canine and first premolar area; corp – corpus; ram – ramus. N.A. – specimen not available. N.S. – not significant.

Table 3
Microstructural analysis of three cortical samples from the buccal side of a female baboon mandible

	Thickness (mm)	Apparent density (mg/cm ³)	E ₃ (GPa)	Orientation of E ₃	E ₁ /E ₃	E ₂ /E ₃	Bone volume fraction (%)	Porosity fraction (%)	Porosity thickness (mm)	Maximum Porosity thickness (mm)
Symphysis (Site B2)	3.80	1831.73	21.2	8.2	0.43	0.50	77.10	22.90	0.202 ± 0.127	0.507
Corpus (Site B11)	2.10	1996.38	24.0	29.0	0.47	0.57	95.54	4.46	0.069 ± 0.054	0.217
Ramus (Site B17)	1.25	2026.86	29.2	42.8	0.62	0.58	97.75	2.25	0.0330 ± 0.014	0.079

Table 4

Comparison of cortical thickness, density, and material properties by area between baboon and human mandibles.

		P	Th	E ₁	E ₂	E ₃	G ₁₂	G ₃₁	G ₂₃	v ₁₂	v ₁₃	v ₂₃	E ₂ /E ₃	
sym	Baboon	Mean	1642	2.9	9.2	11.5	17.3	3.6	4.4	5.5	0.38	0.25	0.19	0.67
		SE	24.9	0.2	0.3	0.4	0.7	0.1	0.2	0.2	0.01	0.01	0.01	0.02
	Human	Mean	1827	2.7	12.0	16.2	20.0	4.7	5.1	6.5	0.20	0.31	0.29	0.84
		SE	18.5	0.1	0.2	0.3	0.6	0.1	0.1	0.1	0.01	0.01	0.01	0.02
C-P ₁	Baboon	Mean	1769	2.1	12.1	14.0	19.2	4.7	5.4	6.4	0.36	0.28	0.21	0.73
		SE	36.6	0.2	0.4	0.7	0.7	0.2	0.2	0.3	0.01	0.01	0.01	0.04
	Human	Mean	1899	2.2	11.6	15.6	20.1	4.7	5.2	7.0	0.16	0.34	0.33	0.81
		SE	15.5	0.1	0.3	0.4	0.8	0.1	0.1	0.2	0.02	0.02	0.02	0.03
corp	Baboon	Mean	1919	2.0	13.2	15.9	25.8	5.2	6.2	7.8	0.37	0.26	0.17	0.63
		SE	13.9	0.1	0.3	0.2	0.4	0.1	0.1	0.1	0.01	0.01	0.01	0.01
	Human	Mean	1959	2.2	12.7	17.8	21.8	5.1	5.6	7.5	0.17	0.34	0.31	0.85
		SE	6.37	0.1	0.1	0.2	0.3	0.0	0.0	0.1	0.01	0.01	0.01	0.01
ram	Baboon	Mean	1956	1.9	12.4	14.6	25.2	4.7	6.0	7.4	0.40	0.24	0.17	0.58
		SE	10.8	0.1	0.3	0.2	0.4	0.1	0.1	0.1	0.01	0.01	0.01	0.01
	Human	Mean	1954	1.9	12.9	18.7	24.4	5.0	5.5	7.5	0.19	0.28	0.26	0.80
		SE	5.6	0.0	0.1	0.1	0.3	0.0	0.0	0.0	0.01	0.01	0.01	0.01

Note: Data of adult male and female baboons are combined; human values were calculated from original data collected by Schwartz-Dabney and Dechow (2003). No sexual dimorphism in material properties of cortical bone were observed in the human mandibles.

Appendix Table 1

Material properties of cortical bone in baboon mandible JMI1.

Specimen JMI	P	Th	E ₁	E ₂	E ₃	G ₁₂	G ₃₁	G ₂₃	v ₁₂	v ₁₃	v ₂₃	E ₂ /E ₃	Axis of E ₃
B1	1421	2.60											103.9
B2	1524	2.84	6.4	10.9	14.9	2.8	2.7	4.7	0.30	0.27	0.26	0.73	110.4
B3	1650	1.68											80.7
B4	1542	1.87	10.4	11.2	11.3	5.2	3.6	4.2	0.05	0.50	0.41	0.99	69.2
B5		0.78											
B6	1559	1.36	7.1	9.6	12.9	3.7	2.5	4.1	0.15	0.43	0.22	0.75	71.0
B7	1663	1.19	8.6	10.4	13.5	4.3	3.0	4.7	0.18	0.49	0.15	0.77	166.4
B8	1497	2.32	6.5	9.2	13.1	5.1	2.2	5.9	0.05	0.55	0.15	0.70	149.2
B9	1746	1.02	9.1	12.2	21.5	3.9	3.8	5.9	0.33	0.29	0.14	0.57	1.6
B10	1621	1.35	7.9	11.0	12.9	4.2	2.8	4.5	0.13	0.44	0.28	0.85	157.2
B11	1796	1.35	10.7	13.9	14.6	5.4	3.8	6.1	0.20	0.51	0.18	0.95	23.1
B12	1829	1.55	12.8	14.0	21.0	5.7	4.9	6.1	0.20	0.40	0.22	0.67	174.7
B13	1746	1.70	11.8	14.2	19.7	6.0	4.4	6.0	0.09	0.39	0.27	0.72	157.1
B14	1796	1.19	9.9	12.8	18.5	4.4	4.0	5.9	0.29	0.37	0.16	0.69	153.2
B15	1796	1.66	11.9	15.0	21.5	5.4	4.8	6.5	0.23	0.33	0.24	0.70	179.0
B16	1746	1.31	10.9	12.5	18.1	4.9	4.1	5.7	0.22	0.42	0.17	0.69	54.3
B17	1842	1.16	10.8	12.5	18.0	4.8	4.2	6.0	0.27	0.42	0.12	0.70	57.2
B18	1478	2.15	6.6	9.1	11.0	3.7	2.2	3.7	0.09	0.48	0.28	0.83	75.7
B19	1497	2.40	7.9	10.3	14.0	4.9	2.9	4.3	0.07	0.41	0.34	0.73	47.4
B20	1633	2.58	7.5	10.6	15.0	3.9	2.8	4.8	0.18	0.37	0.18	0.71	37.5
B21	1478	2.21	6.8	8.2	10.4	3.7	2.4	3.3	0.04	0.46	0.32	0.79	39.3
B22	1347	3.22	5.4	5.8	12.9	2.0	2.5	2.8	0.40	0.25	0.16	0.45	42.8
B23	1518	2.09	7.7	9.8	15.5	4.9	2.8	4.4	0.08	0.40	0.27	0.63	54.5
B24	1535	1.22	6.6	8.9	9.1	4.9	2.3	3.9	0.14	0.59	0.44	0.97	49.1
B25	1612	1.27	7.6	11.7	12.3	4.1	2.7	5.0	0.20	0.46	0.24	0.95	4.7
B26	1445	2.46	3.8	6.1	11.8	1.7	1.5	3.2	0.39	0.31	0.07	0.52	81.3
B27	1573	2.05	6.4	10.4	12.0	4.0	2.1	4.2	0.04	0.44	0.33	0.87	71.6
B28	1663	1.05	6.4	10.1	10.9	3.3	2.4	4.4	0.25	0.47	0.16	0.93	57.5
B29	1397	1.64	5.7	8.5	9.2	4.4	1.9	3.6	0.14	0.54	0.43	0.93	57.7

Specimen JM1	P	Th	E ₁	E ₂	E ₃	G ₁₂	G ₃₁	G ₂₃	v ₁₂	v ₁₃	v ₂₃	E ₂ /E ₃	Axis of E ₃
B30	1568	1.91	6.3	10.0	10.8	4.9	2.3	4.4	0.13	0.48	0.38	0.92	38.3
L1	1596	1.42	7.1	9.0	10.0	4.6	2.5	3.8	0.05	0.53	0.47	0.90	75.4
L2	1497	1.56	4.0	6.1	7.0	5.2	1.8	3.7	0.36	0.60	0.63	0.88	66.6
L3													
L4	1730	1.40	9.9	12.2	17.5	4.8	3.7	5.2	0.16	0.39	0.24	0.70	10.8
L5	1711	1.96	9.2	12.1	21.9	3.8	4.2	5.6	0.31	0.20	0.22	0.55	2.5
L6													
L7	1863	1.33	11.5	14.0	18.0	5.1	4.4	6.0	0.25	0.41	0.23	0.78	20.8
L8	1497	1.33	7.8	11.4	13.9	4.1	2.9	4.8	0.14	0.39	0.26	0.82	172.4
L9	1996	1.45	12.3	15.4	25.3	5.9	4.9	6.6	0.14	0.29	0.25	0.61	5.1
L10	1838	1.64	12.0	13.3	18.4	6.4	4.4	5.5	0.01	0.44	0.31	0.72	10.2
L11	1796	0.97	6.4	10.7	11.3	3.7	2.3	5.0	0.25	0.49	0.08	0.95	174.3
L12	1760	1.38	9.5	12.2	17.8	4.3	3.8	5.8	0.29	0.39	0.13	0.68	163.9
L13	1696	2.03	6.4	9.3	18.2	2.5	3.5	5.5	0.47	0.23	0.09	0.51	18.2
L14	1696	1.70	7.2	11.7	17.3	3.4	2.9	5.6	0.29	0.31	0.15	0.68	8.8
L15	1607	1.45	9.9	12.3	17.6	4.8	3.7	6.1	0.24	0.43	0.09	0.70	0.7
L16	1632	0.90	5.9	10.2	12.1	3.4	2.2	5.3	0.30	0.47	0.01	0.84	85.6
L17	1632	0.91	5.9	10.5	13.1	3.8	2.1	5.6	0.20	0.48	0.13	0.80	87.2
L18	1418	3.07	0.8	1.5	1.7	7.7	1.7	4.8	0.63	0.69	1.00	0.88	113.1
L19	1430	2.35	7.0	8.1	11.8	3.3	2.5	3.2	0.14	0.41	0.29	0.69	138.7
L20	1496	2.78	4.6	7.6	8.2	5.9	1.9	4.3	0.37	0.57	0.55	0.93	151.2
L21	1271	6.00											154.7
L22	1496	2.22	7.6	9.4	12.1	5.5	2.8	4.0	0.19	0.50	0.42	0.78	92.9
Grand Mean	1615.8	1.82	7.9	10.6	14.3	4.4	3.0	4.9	0.21	0.43	0.26	0.76	
S.D.	153.8	0.85	2.5	2.6	4.5	1.1	0.9	1.0	0.13	0.10	0.17	0.13	

Appendix Table 2

Material properties of cortical bone in baboon mandible JM2.

Specimen JM2	P	Th	E ₁	E ₂	E ₃	G ₁₂	G ₃₁	G ₂₃	v ₁₂	v ₁₃	v ₂₃	E ₂ /E ₃	Axis of E ₃
B1	1577	3.20	4.5	8.6	9.8	2.0	2.1	3.9	0.36	0.33	0.16	0.88	111.8
B2	1621	1.80											129.5
B3	1720	2.25	9.8	11.0	17.1	4.2	3.9	4.7	0.23	0.33	0.25	0.65	1.9
B4	1717	1.78	9.3	11.6	13.8	5.9	3.1	5.8	0.04	0.56	0.27	0.84	46.7
B5	1683	1.28	8.6	11.9	13.7	4.3	3.3	4.9	0.16	0.38	0.28	0.87	147.3
B6	1932	1.35	10.9	13.5	18.8	5.5	4.1	5.9	0.12	0.39	0.23	0.72	78.0
B7	1768	1.88	9.6	13.3	15.5	5.4	3.4	5.5	0.08	0.45	0.29	0.86	159.1
B8	1842	1.13	9.3	14.3	16.1	4.8	3.5	6.2	0.20	0.41	0.20	0.89	168.2
B9	1829	1.51	10.3	12.5	26.2	4.2	4.8	6.1	0.32	0.18	0.19	0.48	21.2
B10	1768	1.79	9.4	11.3	14.4	5.7	3.4	4.7	0.06	0.47	0.36	0.79	155.1
B11	1796	2.15	10.6	13.3	17.5	4.5	4.5	5.6	0.27	0.29	0.28	0.76	0.7
B12	1735	1.78	11.2	13.1	18.7	5.3	4.4	5.6	0.15	0.36	0.25	0.70	167.2
B13	1756	2.10	9.8	12.5	15.6	5.0	3.5	5.1	0.12	0.44	0.28	0.80	156.0
B14	1704	2.14	8.5	11.7	13.4	4.2	3.1	4.9	0.20	0.44	0.24	0.87	160.3
B15	1746	1.88	10.7	13.3	20.3	4.9	4.2	5.6	0.20	0.32	0.26	0.66	0.3
B16	1702	1.42	8.6	12.5	18.1	4.9	3.2	5.8	0.09	0.36	0.18	0.69	59.6
B17	1680	1.41	9.0	11.7	13.8	5.2	3.1	4.8	0.03	0.49	0.31	0.85	46.4
B18	1524	2.91	7.0	9.9	13.6	4.6	2.5	4.1	0.08	0.38	0.37	0.73	72.0
B19	1702	1.41	7.6	10.9	14.4	4.4	2.8	4.5	0.03	0.36	0.33	0.76	47.7
B20	1496	1.23	6.6	9.4	12.8	3.5	2.4	4.0	0.13	0.38	0.24	0.73	36.5
B21	1359	2.03	3.5	4.6	5.5	5.2	1.9	3.0	0.53	0.62	0.63	0.83	56.1
B22	1343	1.92	4.3	4.9	6.0	5.4	1.9	3.3	0.43	0.72	0.68	0.82	28.0
B23	1629	2.56	7.5	9.0	13.9	3.0	3.3	4.4	0.36	0.33	0.14	0.65	54.0
B24	1683	1.34	7.8	9.7	12.0	4.3	2.7	3.9	0.04	0.47	0.32	0.81	67.2
B25	1552	1.54	6.5	11.9	12.4	4.2	2.4	5.0	0.04	0.38	0.28	0.96	67.2
B26	1436	2.11	5.3	7.2	8.4	2.5	2.0	3.2	0.29	0.46	0.15	0.85	81.2
B27	1445	2.34	4.5	7.5	9.1	2.3	1.8	3.7	0.32	0.43	0.05	0.83	61.7
B28	1746	1.08	8.1	10.8	14.4	3.9	3.0	4.7	0.21	0.40	0.20	0.75	88.3
B29	1607	1.75	7.0	9.1	12.2	3.3	2.7	3.8	0.20	0.37	0.25	0.74	65.7

Specimen JM2	P	Th	E ₁	E ₂	E ₃	G ₁₂	G ₃₁	G ₂₃	v ₁₂	v ₁₃	v ₂₃	E ₂ /E ₃	Axis of E ₃
B30	1455	2.19	4.9	5.5	7.2	5.2	2.3	3.1	0.46	0.60	0.53	0.77	49.5
L1	1413	2.89	2.4	2.2	3.1	6.0	2.0	2.6	0.68	0.93	1.04	0.70	117.7
L2	1338	3.19	5.3	4.9	9.7	1.7	2.6	2.7	0.55	0.32	0.09	0.50	90.1
L3													
L4	2267	1.11	10.3	18.5	23.2	5.4	4.1	9.1	0.27	0.36	0.09	0.80	12.7
L5	1781	1.16	8.2	11.9	18.9	3.7	3.2	5.3	0.26	0.29	0.21	0.63	4.4
L6	1817	2.42	12.4	13.6	24.7	5.4	5.2	6.3	0.20	0.28	0.18	0.55	157.0
L7	1936	1.57	11.6	14.2	22.2	5.2	4.5	6.4	0.25	0.35	0.19	0.64	171.4
L8	1773	1.47	10.2	12.4	15.4	4.5	3.7	5.4	0.29	0.48	0.18	0.81	3.5
L9	1895	1.80	9.6	12.6	25.3	3.7	4.8	6.2	0.37	0.14	0.22	0.50	3.5
L10	1612	2.08	8.2	10.8	18.8	3.8	3.2	4.8	0.23	0.30	0.20	0.57	5.4
L11	1437	1.84	7.7	12.3	16.8	4.9	2.8	5.4	0.01	0.34	0.28	0.73	3.9
L12	1796	1.53	8.1	12.2	16.2	4.2	3.2	6.4	0.32	0.45	0.01	0.75	176.1
L13	1814	1.01	8.3	12.4	17.1	4.2	3.1	5.8	0.25	0.40	0.12	0.73	7.5
L14	1680	1.58	8.6	12.3	14.6	5.0	3.0	5.8	0.16	0.50	0.12	0.85	23.2
L15	1583	2.28	7.3	11.7	14.0	6.1	2.7	5.3	0.19	0.44	0.43	0.84	1.9
L16	1568	1.80	6.9	13.2	14.9	4.9	2.5	6.2	0.00	0.36	0.22	0.89	120.3
L17	1663	1.23	6.0	11.4	11.8	3.9	2.8	7.8	0.39	0.50	0.26	0.97	125.9
L18	1696	1.69	7.5	13.5	14.6	4.8	2.6	5.7	0.03	0.41	0.37	0.93	119.2
L19	1449	3.24	5.3	8.1	9.0	2.6	2.0	3.2	0.23	0.40	0.31	0.90	133.1
L20	1474	3.80	4.2	4.9	15.3	1.6	6.3	5.1	0.69	0.20	0.26	0.32	140.0
L21	1523	1.59	5.0	8.2	9.5	3.9	2.0	6.6	0.30	0.50	0.31	0.87	165.5
L22	1366	3.65	6.0	8.7	16.1	2.5	2.8	4.4	0.31	0.18	0.17	0.54	121.4
Grand Mean	1655.6	1.93	7.8	10.7	14.7	4.3	3.2	5.1	0.23	0.40	0.27	0.75	
S.D.	180.5	0.67	2.3	3.1	4.9	1.1	1.0	1.3	0.16	0.13	0.17	0.14	

Appendix Table 3

Material properties of cortical bone in baboon mandible JM3.

Specimen JM3	P	Th	E ₁	E ₂	E ₃	G ₁₂	G ₃₁	G ₂₃	v ₁₂	v ₁₃	v ₂₃	E ₂ /E ₃	Axis of E ₃
B1	1645	1.87	7.1	8.0	12.0	2.8	3.0	3.5	0.34	0.31	0.26	0.67	73.9
B2	1623	3.94	5.6	9.9	11.2	2.6	2.6	4.7	0.40	0.38	0.09	0.88	177.5
B3	1810	2.20	8.8	13.0	16.7	3.9	3.7	5.8	0.31	0.33	0.21	0.78	89.6
B4	1841	1.09	9.2	13.7	14.1	4.7	3.3	5.5	0.18	0.44	0.28	0.97	82.5
B5	1870	1.45	8.9	14.9	15.6	4.3	3.6	6.2	0.26	0.36	0.22	0.95	70.5
B6	1828	1.14	10.2	11.1	16.1	4.3	3.7	4.7	0.26	0.46	0.21	0.69	87.2
B7	1923	1.20	10.2	13.9	17.6	5.1	3.8	5.9	0.19	0.40	0.24	0.79	169.7
B8	1695	1.62	9.9	12.3	15.4	4.3	4.0	4.8	0.25	0.31	0.34	0.80	12.3
B9	1915	2.00	12.5	12.8	27.2	4.4	6.2	6.4	0.43	0.20	0.19	0.47	0.0
B10	1795	2.09	11.8	14.0	17.6	4.9	4.6	5.7	0.28	0.37	0.28	0.79	168.9
B11	1675	1.99	8.7	11.7	12.7	4.2	3.2	4.5	0.19	0.42	0.33	0.92	167.6
B12	1955	2.23	12.6	13.5	25.2	4.7	5.9	7.0	0.40	0.29	0.12	0.53	12.0
B13	1781	2.56	10.9	11.9	19.1	4.7	4.5	5.0	0.21	0.28	0.28	0.62	144.7
B14	1828	1.54	11.9	12.9	15.9	4.9	4.4	5.4	0.28	0.45	0.26	0.81	174.8
B15	1787	1.83	9.8	10.7	21.9	3.7	4.4	5.1	0.39	0.25	0.18	0.49	177.2
B16	1760	1.33	9.7	12.3	17.3	4.6	3.6	5.6	0.23	0.42	0.16	0.71	50.5
B17	1784	1.55	10.4	12.0	15.4	4.7	3.8	5.0	0.22	0.44	0.25	0.78	44.1
B18	1496	2.92	8.0	9.7	15.3	3.8	2.9	4.0	0.18	0.37	0.23	0.63	68.1
B19	1932	1.30	10.8	14.0	17.5	5.1	4.0	6.1	0.24	0.44	0.19	0.80	43.8
B20	1645	1.70	7.4	10.0	13.7	3.5	2.8	4.8	0.30	0.43	0.09	0.73	28.1
B21	1745	1.28	9.9	10.9	14.7	5.0	3.7	4.4	0.06	0.42	0.33	0.75	40.8
B22	1415	2.48	3.8	4.3	12.9	1.2	2.3	2.8	0.60	0.18	0.08	0.33	24.4
B23	1525	1.35	7.9	12.8	13.6	4.1	2.6	4.6	0.12	0.40	0.43	0.94	64.4
B24	1596	1.85	6.0	9.5	12.8	3.2	2.1	4.4	0.23	0.41	0.12	0.74	56.1
B25	1683	1.36	6.0	9.2	12.1	3.7	2.1	4.7	0.16	0.50	0.25	0.76	28.8
B26	1444	2.34	3.5	6.1	9.0	1.5	1.5	3.0	0.40	0.32	0.12	0.67	76.5
B27	1368	2.84	4.6	6.8	10.0	2.1	1.9	3.3	0.37	0.36	0.13	0.68	87.1
B28	1496	1.40	6.8	10.0	10.0	4.0	2.4	3.9	0.05	0.48	0.38	1.00	37.9
B29	1813	1.02	7.6	11.1	13.0	3.8	2.9	5.3	0.29	0.47	0.09	0.86	41.4

Specimen JM3	P	Th	E ₁	E ₂	E ₃	G ₁₂	G ₃₁	G ₂₃	v ₁₂	v ₁₃	v ₂₃	E ₂ /E ₃	Axis of E ₃
B30	1674	2.42	9.0	10.6	15.1	4.2	3.6	4.7	0.16	0.35	0.23	0.71	23.5
L1	1567	1.74	6.4	8.5	10.7	3.0	2.5	3.6	0.23	0.38	0.23	0.79	78.9
L2	1396	2.85	5.0	6.1	10.0	2.0	2.3	3.4	0.46	0.37	0.05	0.61	75.0
L3	1745	1.74	8.8	13.3	14.9	5.1	3.2	5.7	0.10	0.43	0.32	0.89	79.9
L4	1889	1.75											96.7
L5	1551	0.90	4.5	8.0	10.6	2.6	2.2	5.3	0.45	0.46	0.17	0.76	168.0
L6	1894	0.95	7.1	13.5	14.0	3.5	3.0	6.1	0.33	0.39	0.11	0.97	147.1
L7	1841	1.20	8.1	14.1	15.6	3.9	3.4	6.5	0.31	0.38	0.13	0.91	170.4
L8	2047	1.84	11.1	14.1	25.9	4.4	5.1	6.8	0.38	0.24	0.20	0.55	178.6
L9	1994	1.21	7.0	9.5	26.9	2.7	4.9	5.7	0.50	0.10	0.30	0.35	4.9
L10	1745	2.31	9.4	9.8	19.9	3.4	4.3	4.6	0.42	0.26	0.19	0.49	6.7
L11	1654	2.20	8.6	10.2	22.0	3.2	4.3	5.5	0.43	0.21	0.14	0.46	1.8
L12	1784	1.57	9.8	12.8	24.7	4.2	4.2	5.7	0.25	0.19	0.24	0.52	1.6
L13	1764	1.12	7.3	9.7	15.3	3.0	3.2	4.5	0.36	0.30	0.19	0.63	19.4
L14	1781	1.15	8.6	10.0	16.9	3.5	3.4	4.5	0.33	0.35	0.19	0.59	23.8
L15	1745	1.56	8.8	9.7	13.5	4.2	3.1	3.7	0.09	0.43	0.36	0.72	171.3
L16	1745	1.47	8.0	12.3	15.7	4.9	3.0	5.2	0.01	0.36	0.32	0.79	115.7
L17	1709	1.13	6.6	10.7	15.3	3.0	3.2	5.9	0.42	0.34	0.03	0.70	105.6
L18	1615	1.68	7.3	13.5	13.9	4.6	2.7	5.5	0.04	0.38	0.35	0.97	140.0
L19	1596	1.16	7.3	10.3	13.2	3.7	2.8	5.0	0.24	0.43	0.10	0.78	137.1
L20	1546	1.71	6.2	7.2	9.4	5.1	2.6	3.5	0.32	0.52	0.44	0.76	171.1
L21	1396	2.98	3.8	4.0	9.9	1.3	2.1	2.6	0.58	0.30	0.01	0.40	179.2
L22	1638	1.31	4.0	6.6	16.8	1.6	2.8	4.1	0.46	0.12	0.31	0.39	124.3
Grand Mean	1711.3	1.76	8.1	10.7	15.6	3.7	3.4	4.9	0.29	0.36	0.21	0.71	
S.D.	162.3	0.63	2.3	2.7	4.5	1.1	1.0	1.0	0.14	0.10	0.10	0.17	

Appendix Table 4

Material properties of cortical bone in baboon mandible AF1.

Specimen	AF1	P	Th	E ₁	E ₂	E ₃	G ₁₂	G ₃₁	G ₂₃	v ₁₂	v ₁₃	v ₂₃	E ₂ /E ₃	Axis of E ₃
B1		1611	2.13	8.1	11.7	13.3	3.8	3.3	5.3	0.25	0.36	0.16	0.88	109.3
B2		1618	3.47	9.0	10.7	17.1	3.4	4.3	5.4	0.40	0.26	0.16	0.63	80.4
B3		1582	5.59	7.1	10.8	12.5	3.0	3.3	5.2	0.41	0.34	0.11	0.86	55.4
B4		1781	1.24	10.5	15.6	17.0	5.9	3.9	6.9	0.13	0.45	0.26	0.91	143.9
B5		1940	1.50	12.4	17.7	18.4	5.9	4.9	7.3	0.22	0.37	0.24	0.96	92.0
B6		1717	3.34	10.0	12.2	19.0	3.9	4.7	6.1	0.40	0.29	0.15	0.64	27.8
B7		1995	1.27	11.3	14.8	20.5	5.3	4.5	6.8	0.24	0.36	0.17	0.72	4.4
B8		1819	1.37	8.8	16.8	16.8	4.2	4.0	7.6	0.31	0.34	0.11	1.00	37.8
B9		1924	2.03	11.1	12.4	25.2	4.2	5.4	6.5	0.40	0.23	0.14	0.49	1.3
B10		1948	1.78	12.7	16.3	22.0	5.9	5.2	7.3	0.21	0.33	0.21	0.74	164.1
B11		1853	1.65	11.2	13.5	21.1	4.7	4.7	6.4	0.32	0.33	0.16	0.64	34.1
B12		2045	1.57	14.0	14.9	24.0	5.7	5.9	8.0	0.35	0.39	0.05	0.62	8.4
B13		1880	1.93	13.3	16.7	23.2	6.0	5.4	7.1	0.22	0.31	0.26	0.72	179.6
B14		1853	1.57	12.1	18.5	19.3	6.2	4.6	7.9	0.22	0.43	0.20	0.96	144.5
B15		2086	1.68	14.5	19.3	25.1	6.4	6.0	8.8	0.30	0.36	0.18	0.77	163.5
B16		1995	1.63	13.2	18.1	22.0	6.0	5.4	8.3	0.29	0.38	0.16	0.82	64.1
B17		2043	1.74	13.1	18.1	21.9	5.9	5.4	8.4	0.30	0.38	0.14	0.82	57.7
B18		2072	1.25	14.0	17.2	21.1	6.2	5.3	7.8	0.29	0.46	0.15	0.81	70.9
B19		1995	1.40	14.4	17.9	23.1	6.8	5.5	8.2	0.23	0.42	0.16	0.78	60.1
B20		2078	1.13	12.9	18.6	24.4	6.1	5.2	8.7	0.28	0.37	0.14	0.76	40.8
B21		2078	1.28	12.5	15.2	23.9	5.1	5.6	7.8	0.37	0.32	0.12	0.64	36.1
B22		2078	1.75	12.6	15.9	18.0	5.9	4.7	6.5	0.21	0.43	0.27	0.88	29.5
B23		2078	2.54	14.5	15.4	28.0	5.5	6.6	7.5	0.36	0.26	0.17	0.55	34.6
B24		1878	1.37	11.0	15.7	19.7	5.2	4.5	6.9	0.22	0.33	0.21	0.80	45.5
B25		2078	1.48	12.5	18.0	20.7	5.6	5.2	7.9	0.30	0.36	0.19	0.87	167.3
B26		2078	2.71	13.2	17.3	21.0	6.0	5.3	7.3	0.25	0.36	0.26	0.82	81.9
B27		1819	1.40	8.4	12.6	24.0	3.3	4.3	6.6	0.38	0.15	0.18	0.52	73.5
B28		1936	1.38	11.5	14.7	25.0	5.0	5.1	7.1	0.28	0.26	0.17	0.59	70.0
B29		1995		10.4	17.6	18.3	5.2	4.1	6.6	0.16	0.33	0.39	0.96	77.7

Specimen	AF1	P	Th	E ₁	E ₂	E ₃	G ₁₂	G ₃₁	G ₂₃	v ₁₂	v ₁₃	v ₂₃	E ₂ /E ₃	Axis of E ₃
B30		1829	1.08	9.3	12.3	23.4	3.9	4.2	6.3	0.34	0.25	0.12	0.52	59.7
L1		1477	2.03	7.1	9.4	12.0	3.5	2.6	4.1	0.21	0.44	0.18	0.78	109.5
L2		1497	1.94	7.4	11.4	13.3	4.0	2.7	5.0	0.17	0.43	0.29	0.86	74.8
L3		1549	3.00	8.0	10.6	15.8	3.2	3.7	5.1	0.37	0.28	0.16	0.67	108.5
L4		1821	1.70	11.8	15.0	22.4	5.1	4.9	6.9	0.30	0.32	0.19	0.67	173.7
L5		1853	1.63	13.5	16.7	21.5	6.4	5.2	7.2	0.19	0.39	0.24	0.78	3.0
L6		1650	1.98	11.2	13.7	20.8	4.6	4.8	6.2	0.31	0.30	0.22	0.66	161.9
L7		1770	2.35	11.1	14.7	19.4	5.3	4.2	6.2	0.21	0.38	0.25	0.76	3.6
L8		1819	1.38	11.4	15.7	22.5	4.9	5.0	7.4	0.33	0.31	0.17	0.70	3.9
L9			0.65											
L10		1755	2.29	11.3	12.6	20.5	4.6	4.7	5.6	0.30	0.30	0.23	0.61	2.1
L11		1933	1.57	12.5	16.7	21.0	5.6	5.0	7.3	0.28	0.38	0.22	0.80	166.5
L12		1885	1.50	12.0	15.9	25.7	5.0	5.4	7.3	0.31	0.24	0.22	0.62	6.7
L13		1853	1.66	11.2	14.6	21.7	4.5	5.0	7.0	0.37	0.30	0.17	0.67	32.2
L14		1819	1.34	10.7	14.2	17.0	4.9	4.3	5.9	0.24	0.35	0.26	0.83	178.1
L15		1765	1.59	11.8	17.8	19.2	5.5	4.7	7.2	0.24	0.35	0.27	0.93	161.6
L16		1829	1.98	11.3	13.5	21.6	4.5	5.0	6.5	0.36	0.31	0.17	0.63	90.9
L17			0.78											
L18		1796	1.23	8.6	12.3	15.6	4.0	3.4	5.1	0.22	0.34	0.27	0.78	107.1
L19		1896	0.86	6.8	12.1	16.4	3.2	3.2	6.5	0.38	0.34	0.03	0.74	156.8
L20		1723	1.69	10.6	13.0	17.4	4.7	4.2	6.3	0.29	0.40	0.12	0.75	151.5
L21		1702	1.45	9.5	11.6	15.5	4.2	3.7	5.1	0.25	0.38	0.22	0.75	156.8
L22		1842	1.16	10.5	15.1	18.7	5.1	4.1	6.5	0.22	0.36	0.22	0.81	148.6
Grand Mean		1858.3	1.77	11.2	14.9	20.1	5.0	4.6	6.8	0.28	0.34	0.19	0.75	
S.D.		161.9	0.79	2.1	2.5	3.6	1.0	0.8	1.0	0.07	0.06	0.06	0.12	

Appendix Table 5

Material properties of cortical bone in baboon mandible AF2.

Specimen	AF2	P	Th	E ₁	E ₂	E ₃	G ₁₂	G ₃₁	G ₂₃	v ₁₂	v ₁₃	v ₂₃	E ₂ /E ₃	Axis of E ₃
B1		1698	3.09	10.3	17.2	17.2	4.3	4.9	6.5	0.31	0.22	0.30	1.00	57.1
B2		1788	2.48	11.1	13.9	20.1	4.8	4.7	6.5	0.30	0.33	0.18	0.69	73.6
B3		1828	1.71	10.9	15.5	16.7	6.3	4.1	6.4	0.04	0.42	0.32	0.93	84.1
B4		1584	2.92	10.1	14.4	14.9	4.8	3.9	5.5	0.21	0.37	0.34	0.97	84.7
B5		1899	1.80	13.7	16.2	19.4	5.5	5.7	7.3	0.35	0.35	0.19	0.83	96.0
B6		1801	2.41	13.2	13.1	20.7	4.8	5.8	6.2	0.39	0.30	0.19	0.64	68.1
B7		1706	2.96	10.9	14.5	21.5	4.9	4.4	6.1	0.22	0.28	0.27	0.67	175.8
B8		1994	1.26	11.8	17.1	18.5	5.8	4.5	7.6	0.26	0.44	0.20	0.92	63.7
B9		1994	1.49	15.4	17.5	30.0	6.3	6.6	8.0	0.29	0.27	0.21	0.58	175.8
B10		1866	2.46	13.4	16.1	28.1	5.4	6.0	7.7	0.32	0.26	0.19	0.58	7.5
B11		2044	1.55	13.4	21.3	23.5	5.8	6.0	8.6	0.30	0.27	0.28	0.91	74.2
B12		1953	1.86	15.7	20.5	22.1	8.0	5.8	8.9	0.16	0.45	0.21	0.93	176.7
B13		1994	1.83	14.5	21.1	24.9	7.0	5.8	8.3	0.18	0.32	0.32	0.84	164.4
B14		1951	1.82	15.0	17.8	28.5	6.5	6.1	8.0	0.27	0.33	0.20	0.63	168.6
B15		2032	2.07	16.0	20.1	28.8	7.7	6.1	8.7	0.16	0.36	0.23	0.70	157.7
B16		1904	1.62	16.0	19.0	27.5	7.1	6.5	8.3	0.22	0.33	0.23	0.69	81.4
B17		1994	1.45	16.9	18.5	25.3	7.3	6.6	8.4	0.24	0.39	0.18	0.73	52.0
B18		2025	2.64	17.1	18.2	31.6	6.4	7.8	8.4	0.35	0.24	0.23	0.58	84.3
B19		2053	1.37	15.5	18.4	24.3	6.7	6.2	8.5	0.29	0.40	0.15	0.76	45.1
B20		2068	2.17	15.8	18.2	26.3	6.8	6.4	8.5	0.27	0.37	0.17	0.69	37.3
B21		1994	1.08	12.0	15.9	19.6	5.7	4.6	7.7	0.32	0.48	0.07	0.81	33.3
B22		1795	1.60	11.0	14.1	25.6	4.6	5.1	6.6	0.29	0.18	0.23	0.55	19.7
B23		1962	2.37	15.4	19.5	24.1	6.9	6.1	7.9	0.22	0.35	0.29	0.81	64.4
B24		1936	1.29	11.6	17.4	24.6	5.3	5.0	8.0	0.27	0.29	0.20	0.71	19.8
B25		1864	1.73	14.6	16.5	19.8	6.9	5.3	7.1	0.16	0.47	0.23	0.83	155.4
B26		1994	1.42	13.2	17.0	25.2	5.7	5.4	7.6	0.30	0.33	0.20	0.67	87.3
B27		2029	2.36	14.8	19.7	30.7	6.3	6.5	9.2	0.30	0.27	0.20	0.64	80.7
B28		1852	1.20	10.7	14.6	20.2	6.1	3.7	5.8	0.03	0.39	0.34	0.72	79.3
B29		2061	1.24	13.1	19.1	22.2	5.8	5.4	8.5	0.35	0.39	0.17	0.86	118.0

Specimen AF2	P	Th	E ₁	E ₂	E ₃	G ₁₂	G ₃₁	G ₂₃	v ₁₂	v ₁₃	v ₂₃	E ₂ /E ₃	Axis of E ₃
B30	2066	1.28	12.6	16.3	29.1	5.0	6.0	8.0	0.35	0.21	0.19	0.56	29.9
L1	1679	1.64	8.9	13.7	13.9	5.6	3.2	5.5	0.01	0.46	0.36	0.99	161.2
L2	1918	1.10	10.9	15.1	21.1	4.7	4.7	6.7	0.30	0.30	0.22	0.71	74.7
L3	1709	2.18	10.8	13.9	24.1	4.7	4.7	6.2	0.26	0.21	0.25	0.58	64.3
L4	1822	2.16	13.4	17.9	23.8	5.5	6.1	7.7	0.32	0.25	0.26	0.75	134.5
L5	1951	1.88	15.3	17.2	28.3	5.9	6.8	8.2	0.37	0.30	0.18	0.61	173.7
L6	1625	4.36	13.0	15.6	25.5	5.4	6.1	7.0	0.28	0.19	0.26	0.61	164.2
L7	1709	2.69	9.1	10.4	23.4	3.1	5.3	6.3	0.56	0.21	0.11	0.44	176.5
L8	1945	1.57	16.5	18.0	24.8	7.1	6.3	8.0	0.24	0.41	0.20	0.73	172.1
L9	1864	1.90	14.3	18.0	28.4	6.2	6.3	9.1	0.30	0.30	0.11	0.63	173.1
L10	1737	2.51	11.6	14.2	25.6	4.6	5.2	6.8	0.36	0.27	0.18	0.55	172.4
L11	2193	1.21	15.7	18.2	27.1	6.6	6.3	8.8	0.35	0.42	0.11	0.67	1.1
L12	2081	1.78	15.4	18.4	31.5	6.1	6.8	8.7	0.36	0.28	0.19	0.58	3.9
L13	1757	3.50	11.8	13.6	25.4	4.4	5.8	7.3	0.45	0.27	0.12	0.53	2.1
L14	1880	1.51	11.5	17.7	19.0	5.1	4.7	6.8	0.27	0.33	0.33	0.93	21.3
L15	2094	1.70	12.9	18.5	27.4	5.4	5.8	8.8	0.36	0.29	0.18	0.68	11.6
L16	1908	1.88	11.5	15.3	25.1	4.5	5.4	7.0	0.36	0.21	0.25	0.61	97.1
L17	2071	1.16	12.1	15.8	19.0	5.1	4.9	7.0	0.37	0.42	0.18	0.83	121.5
L18	2050	1.53	15.9	17.9	25.6	6.5	6.3	8.3	0.33	0.41	0.15	0.70	103.9
L19	1920	2.18	13.2	15.8	21.1	5.4	5.3	6.7	0.32	0.35	0.26	0.75	116.1
L20	2112	1.45	13.5	14.5	28.1	5.0	6.2	7.2	0.40	0.28	0.15	0.51	157.7
L21	1813	1.78	11.4	15.9	16.5	5.5	4.3	6.2	0.20	0.42	0.30	0.96	173.0
L22	2094	0.91	8.6	14.1	17.3	4.2	3.7	7.3	0.40	0.44	0.02	0.82	132.7
Grand Mean	1916.6	1.91	13.1	16.7	23.7	5.7	5.5	7.5	0.29	0.33	0.21	0.72	
S.D.	140.2	0.67	2.2	2.3	4.4	1.0	0.9	1.0	0.10	0.08	0.07	0.14	

Appendix Table 6

Material properties of cortical bone in baboon mandible AM1.

Specimen	AM1	P	Th	E ₁	E ₂	E ₃	G ₁₂	G ₃₁	G ₂₃	v ₁₂	v ₁₃	v ₂₃	E ₂ /E ₃	Axis of E ₃
B1		1433	5.73	8.7	7.9	14.7	2.9	4.4	3.8	0.47	0.17	0.25	0.54	93.4
B2		1733	3.14	11.9	11.8	16.3	4.2	5.3	5.3	0.42	0.27	0.26	0.73	91.8
B3		1663	4.43	7.5	9.9	17.5	2.8	4.5	6.4	0.55	0.27	0.03	0.57	82.7
B4		1663	2.78	11.5	14.1	17.4	4.4	5.1	6.1	0.38	0.28	0.26	0.81	169.6
B5		1770	2.27	12.1	14.6	21.5	4.8	5.7	6.8	0.34	0.23	0.21	0.68	105.7
B6		1881	2.50	15.2	19.1	19.9	6.5	6.2	7.5	0.26	0.33	0.30	0.96	28.6
B7		1889	2.23	13.5	15.6	19.1	5.9	5.5	6.2	0.21	0.33	0.32	0.82	93.7
B8		2051	1.42	14.3	17.8	29.6	6.2	6.2	8.3	0.28	0.28	0.19	0.60	172.7
B9		1995	2.55	15.7	16.4	31.5	5.9	7.3	7.9	0.35	0.23	0.19	0.52	178.4
B10		1829	2.36	13.2	16.5	21.4	5.3	6.0	6.9	0.32	0.24	0.30	0.77	158.3
B11		1966	2.40	12.9	19.5	20.5	6.1	5.1	8.2	0.26	0.39	0.22	0.95	36.1
B12		1824	2.61	12.2	15.7	21.6	5.1	5.2	7.1	0.32	0.32	0.20	0.73	176.7
B13		1874	2.51	14.3	15.3	22.8	6.0	6.0	6.5	0.22	0.28	0.28	0.67	164.0
B14		2035	1.91	15.7	20.1	27.1	6.6	6.9	8.7	0.29	0.28	0.25	0.74	150.6
B15		2032	2.06	13.4	19.8	24.0	6.6	5.2	8.6	0.22	0.38	0.21	0.83	155.1
B16		1916	1.90	11.7	16.5	29.8	4.8	6.1	7.7	0.31	0.08	0.28	0.56	80.9
B17		1910	2.60	12.9	15.9	24.5	4.9	6.4	7.4	0.38	0.20	0.25	0.65	59.4
B18		1995	1.30	14.8	17.1	25.5	6.5	5.9	7.8	0.24	0.36	0.18	0.67	58.5
B19		1916	1.90	11.7	16.2	28.8	4.8	6.1	7.7	0.31	0.10	0.26	0.56	64.3
B20		1940	2.63	8.6	11.9	17.1	3.8	3.5	5.5	0.34	0.37	0.16	0.70	38.0
B21		1796	2.45	10.3	13.0	19.9	4.4	4.2	5.9	0.29	0.33	0.20	0.65	40.2
B22		1811	2.09	12.1	14.2	20.4	5.0	5.1	6.3	0.30	0.32	0.23	0.70	27.5
B23		1912	2.71	11.9	15.5	21.8	4.7	5.4	7.0	0.36	0.26	0.24	0.71	60.7
B24		1954	1.92	11.6	18.8	20.8	5.4	5.1	7.5	0.23	0.26	0.29	0.90	19.5
B25		1960	2.13	12.3	17.5	25.2	5.4	5.2	7.7	0.27	0.27	0.25	0.70	116.2
B26		1909	1.84	11.7	17.1	23.0	5.3	5.1	7.4	0.24	0.26	0.25	0.74	110.4
B27		1960	2.24	12.5	17.1	25.4	5.2	5.5	7.5	0.33	0.26	0.25	0.67	102.7
B28		2062	2.41	11.6	16.6	27.0	4.9	5.3	7.9	0.31	0.23	0.20	0.62	95.6
B29		1865	1.74	10.4	18.3	17.6	5.2	4.1	6.6	0.16	0.33	0.39	1.04	100.1

Specimen AM1	P	Th	E ₁	E ₂	E ₃	G ₁₂	G ₃₁	G ₂₃	v ₁₂	v ₁₃	v ₂₃	E ₂ /E ₃	Axis of E ₃
B30	1950	1.83	12.1	17.5	24.4	5.6	5.0	7.5	0.23	0.29	0.25	0.72	48.7
L1	1512	2.34	7.1	11.0	12.9	3.4	3.0	4.4	0.19	0.27	0.30	0.86	94.2
L2	1556	3.09	7.4	10.5	13.7	3.2	3.2	4.9	0.34	0.32	0.17	0.77	103.7
L3	1515	3.80	7.5	8.9	13.0	3.0	3.3	4.4	0.40	0.36	0.13	0.69	111.0
L4	1960	2.21	14.9	16.9	27.2	6.4	6.3	7.7	0.23	0.29	0.20	0.62	160.8
L5	2053	1.38	13.9	19.0	24.8	6.1	5.9	8.3	0.28	0.31	0.23	0.77	6.8
L6	1958	2.21	14.6	16.4	30.3	5.5	7.4	8.1	0.38	0.17	0.21	0.54	179.4
L7	1961	2.42	14.9	16.8	29.7	5.7	7.1	8.1	0.36	0.22	0.20	0.56	167.4
L8	2162	1.57	16.4	19.6	32.4	6.9	7.0	9.3	0.30	0.30	0.17	0.60	173.6
L9	2106	1.59	15.7	18.0	31.9	6.3	6.9	8.8	0.34	0.29	0.15	0.57	173.9
L10	1962	2.51	14.4	19.9	26.0	6.9	5.7	8.2	0.19	0.32	0.28	0.76	162.0
L11	2058	1.37	14.3	19.0	24.1	6.3	5.9	9.2	0.34	0.40	0.10	0.79	162.2
L12	2082	1.85	13.5	19.2	28.9	5.7	6.1	8.7	0.31	0.24	0.23	0.67	1.7
L13	1810	3.44	12.7	17.3	23.3	5.6	5.8	7.0	0.23	0.20	0.33	0.74	0.9
L14	2195	1.36	13.4	17.5	29.1	5.2	6.5	8.9	0.40	0.24	0.16	0.60	2.6
L15	2095	1.72	15.2	21.6	27.1	7.0	6.4	9.4	0.24	0.31	0.23	0.80	160.8
L16	1892	2.56	13.1	15.0	23.4	5.1	5.8	7.0	0.37	0.31	0.20	0.64	94.9
L17	2217	1.02	13.5	19.4	24.0	6.4	5.4	9.1	0.29	0.41	0.13	0.81	113.8
L18	1948	1.85	14.0	16.0	25.5	5.7	6.2	7.1	0.28	0.25	0.24	0.63	113.8
L19	1995	1.88	13.1	15.5	28.3	5.1	6.7	7.9	0.37	0.18	0.17	0.55	144.5
L20	1947	3.36	14.3	17.7	27.5	5.8	6.6	8.1	0.32	0.24	0.23	0.64	105.9
L21	1995	2.34	13.1	16.2	23.0	5.3	5.8	7.6	0.36	0.31	0.18	0.70	84.8
L22	2037	2.00	13.0	18.7	25.5	5.9	5.5	8.2	0.26	0.29	0.24	0.74	112.9
Grand Mean	1913.7	2.32	12.7	16.3	23.6	5.3	5.6	7.4	0.31	0.28	0.22	0.70	
S.D.	166.8	0.80	2.2	3.0	5.0	1.0	1.0	1.3	0.07	0.07	0.06	0.11	

Appendix Table 7

Material properties of cortical bone in baboon mandible AM2.

Specimen AM2	P	Th	E ₁	E ₂	E ₃	G ₁₂	G ₃₁	G ₂₃	v ₁₂	v ₁₃	v ₂₃	E ₂ /E ₃	Axis of E ₃
B1	1524	2.68	9.5	11.6	12.5	4.5	3.5	4.8	0.18	0.43	0.26	0.92	98.7
B2	1734	2.15	5.7	9.8	18.6	2.2	4.8	5.9	0.45	0.12	0.33	0.53	82.5
B3	1779	2.84	9.8	17.2	18.0	5.0	4.3	8.5	0.30	0.37	0.03	0.95	103.4
B4		0.77											
B5		0.88											
B6	1834	2.63	12.7	12.4	20.2	4.6	5.6	6.0	0.38	0.30	0.17	0.61	64.7
B7	1928	1.38	12.5	15.1	20.6	6.0	4.8	6.8	0.17	0.39	0.19	0.73	179.5
B8	1870	2.65	14.5	17.1	24.9	6.2	6.1	7.9	0.27	0.32	0.19	0.69	168.7
B9	1995	1.60	12.3	19.3	23.5	5.5	5.4	9.1	0.33	0.33	0.14	0.82	169.9
B10	1936	1.72	11.5	15.4	24.6	5.5	4.5	7.2	0.22	0.34	0.16	0.63	13.0
B11	1829	2.07	12.7	16.6	18.0	6.5	4.7	6.5	0.13	0.41	0.39	0.92	84.1
B12	1932	1.53	12.6	17.0	23.4	5.3	5.7	8.0	0.32	0.28	0.17	0.73	175.8
B13	1995	2.54	12.8	15.1	24.8	5.2	5.7	7.2	0.33	0.28	0.18	0.61	159.3
B14	1857	3.54	24.0	16.2	20.4	12.2	6.3	8.3	0.13	0.79	0.43	0.79	148.6
B15	2024	3.05	15.6	17.5	26.8	6.8	6.3	8.0	0.22	0.35	0.19	0.65	161.2
B16	1853	1.72	13.5	16.8	23.2	6.8	5.2	7.7	0.15	0.39	0.19	0.73	71.2
B17	2026	2.89	11.2	14.6	24.7	4.4	5.5	7.5	0.41	0.26	0.15	0.59	54.9
B18	2038	2.03	14.5	16.0	25.5	6.7	5.9	6.8	0.14	0.30	0.27	0.63	67.9
B19	1904	1.83	14.2	16.2	26.0	6.4	6.0	7.6	0.19	0.30	0.18	0.63	55.1
B20	1924	2.48	13.8	13.6	28.0	4.9	6.9	7.1	0.42	0.21	0.16	0.49	42.6
B21	1995	2.20	10.9	11.3	20.9	4.0	5.0	5.7	0.41	0.29	0.15	0.54	36.0
B22	1733	3.33	12.0	12.0	17.6	9.5	5.6	6.0	0.37	0.47	0.42	0.68	26.0
B23	1995	2.39	14.3	15.4	23.7	6.7	5.6	6.4	0.10	0.35	0.28	0.65	68.1
B24	1936	1.74	11.7	16.5	20.0	5.6	4.7	7.0	0.20	0.34	0.25	0.83	11.2
B25	1995	1.60	10.1	12.3	17.4	4.7	3.8	5.4	0.21	0.41	0.20	0.70	156.9
B26	2062	2.68	9.3	11.9	23.4	3.6	4.6	6.6	0.46	0.27	0.10	0.51	90.6
B27	1953	2.04	9.3	14.9	28.7	4.0	4.7	6.9	0.27	0.01	0.30	0.52	98.2
B28	2057	1.53	11.2	17.0	24.5	5.2	4.7	7.6	0.24	0.27	0.22	0.69	79.5
B29	2062	1.38	11.9	14.1	27.3	4.6	5.7	6.7	0.35	0.17	0.22	0.52	46.9

Specimen	AM2	P	Th	E ₁	E ₂	E ₃	G ₁₂	G ₃₁	G ₂₃	v ₁₂	v ₁₃	v ₂₃	E ₂ /E ₃	Axis of E ₃
B30		1968	3.44	15.4	15.2	29.1	5.5	7.5	8.0	0.40	0.23	0.13	0.52	42.2
L1		1650	2.11	11.1	12.7	15.8	5.1	4.3	5.9	0.21	0.42	0.16	0.81	98.0
L2		1705	2.57	11.8	12.8	19.6	5.4	4.8	5.5	0.13	0.33	0.26	0.65	83.7
L3		1645	4.57	8.4	9.8	17.8	3.0	4.6	5.5	0.50	0.21	0.13	0.55	79.0
L4		1842	2.24	11.1	15.9	16.1	5.5	4.1	6.3	0.19	0.42	0.30	0.99	176.8
L5		2038	1.99	15.6	16.2	28.3	5.8	7.2	7.9	0.37	0.26	0.18	0.57	167.9
L6		1496	1.68	12.1	14.5	20.0	6.0	4.6	6.4	0.13	0.40	0.22	0.73	173.7
L7		1765	2.19	12.4	14.4	23.7	5.3	5.5	6.5	0.23	0.24	0.22	0.61	5.9
L8		1796	3.48	14.2	18.2	19.3	10.8	5.7	8.4	0.21	0.49	0.39	0.95	4.2
L9		2059	2.94	13.3	15.3	27.6	5.0	6.3	7.7	0.41	0.26	0.16	0.55	177.4
L10		1995	2.03	15.1	17.1	26.4	6.6	6.3	7.7	0.22	0.31	0.21	0.65	10.1
L11		1884	1.63	13.3	17.2	22.1	5.7	5.6	7.5	0.30	0.32	0.23	0.78	31.1
L12		1935	2.88	12.9	16.2	20.2	11.5	5.7	8.1	0.33	0.49	0.45	0.80	4.7
L13		1853	2.42	11.4	17.1	20.2	5.1	5.1	8.4	0.36	0.36	0.08	0.85	163.4
L14		1952	2.06	12.7	20.2	22.4	6.2	5.4	8.3	0.20	0.29	0.27	0.90	9.0
L15		1.54												
L16		1770	2.74	12.5	15.8	21.2	5.9	5.6	9.7	0.34	0.39	0.08	0.75	107.3
L17		1904	1.11	9.6	11.9	21.6	3.7	4.6	5.8	0.40	0.21	0.22	0.55	133.2
L18		1995	3.40	7.9	11.0	18.9	3.2	3.8	6.0	0.44	0.31	0.09	0.58	95.3
L19		1961	2.75	11.9	12.5	21.8	4.2	5.9	6.1	0.44	0.21	0.22	0.57	150.2
L20		1967	2.72	8.7	10.4	20.4	3.3	3.8	4.9	0.41	0.26	0.19	0.51	142.1
L21		1969	3.07	10.6	10.4	23.0	3.6	5.2	5.7	0.47	0.27	0.09	0.45	155.2
L22		2082	1.87	15.0	15.0	21.2	7.9	5.4	7.2	0.01	0.49	0.20	0.71	152.5
Grand Mean		1898.0	2.29	12.3	14.8	22.1	5.7	5.3	7.0	0.29	0.32	0.21	0.68	
S.D.		137.2	0.75	2.7	2.5	3.7	2.0	0.9	1.1	0.12	0.12	0.09	0.14	